Understanding Cooperative Intergroup Aggression in Vervet Monkeys: the Importance of Resource-Based Benefits and Social Incentives

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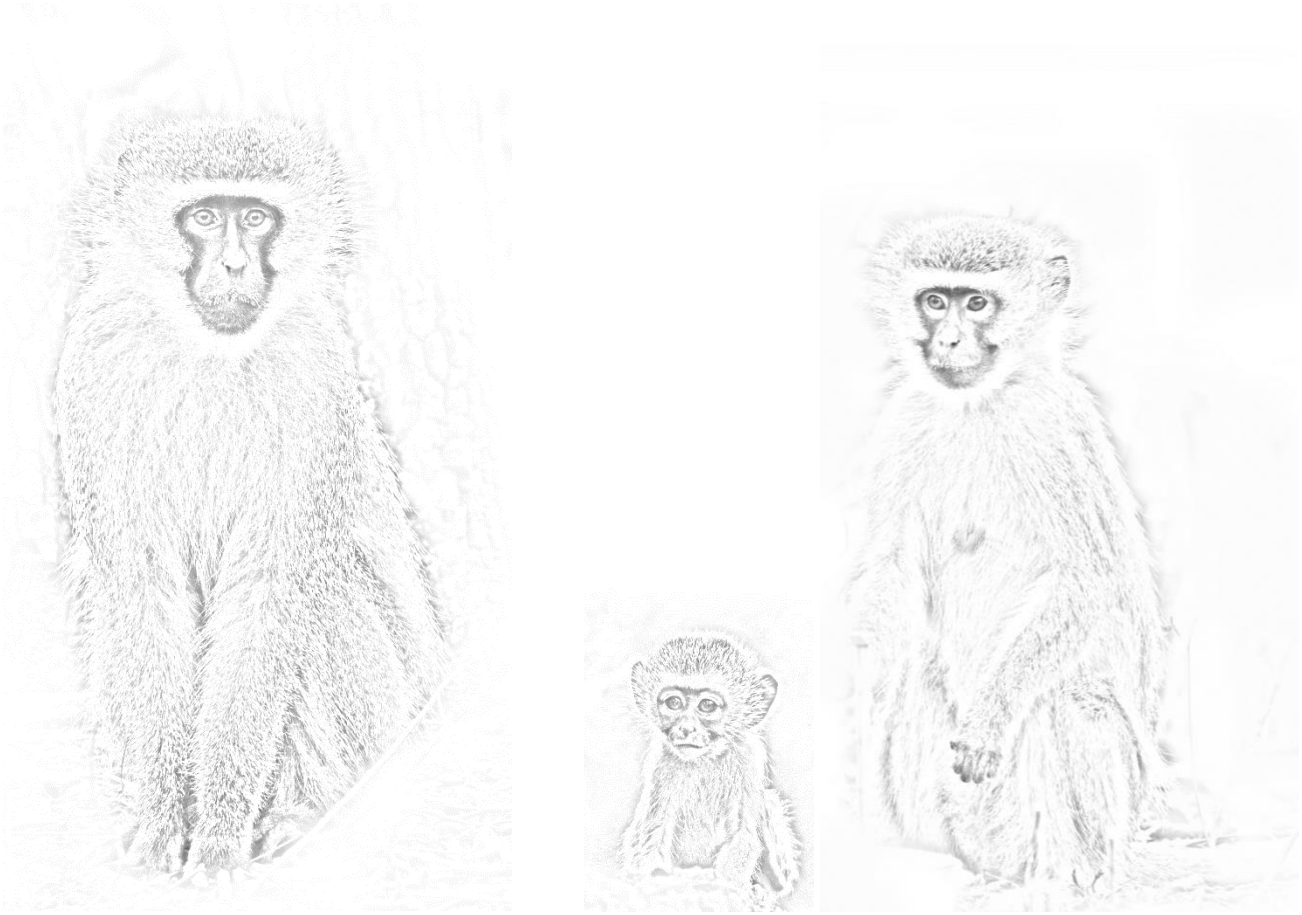

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SUMMARY

Groups of social animals are typically a collection of selfish individuals, who each gain different benefits and experience different costs from group life. As a result, individual group members often exhibit different fitness-maximizing strategies, and the patterns of cooperative behaviour that emerge at the group level can be highly dynamic, and context specific, depending on the benefits at stake, the risks associated with the cooperative activity, and the conflicts of interest that arise among individual group members. It is therefore, critical to understand the factors influencing individual decisions when investigating the evolutionary mechanisms driving group-level patterns of cooperation. The goal of this dissertation was to understand the variety of, and interplay among, fitness-maximizing strategies employed by vervet monkeys (*Chlorocebus aethiops pygerythrus*) in the context of cooperative intergroup aggression. To do so, we examine the resource-based benefits that males and females each stand to gain from participating in aggressive intergroup conflicts, identify the conflicts of interest that arise between group members, and investigate the manipulative strategies that males and females use to resolve these conflicts and achieve more self-serving outcomes.

By examining the causes of intra- and interindividual variability in participation in intergroup conflicts, we could show that females and males fight for different resource-based benefits, and have different strategies for managing the risks associated with intergroup conflicts. Females fight to defend access to valuable food resources, as well as intensely used areas of their home range. Conversely, males fight to protect offspring, as well as to support females when doing so is associated with greater mating success (i.e. during the mating season). The latter finding highlights that because female vervet monkeys are able to exert female choice, they can leverage mating opportunities for male cooperation in intergroup conflicts. Both males and females appear sensitive to the risk of attacks on infants during escalated intergroup conflicts; however, females with infants tend to manage this risk by avoiding the front-line, while males who are likely sires stay at the front-line to monitor the encounter and respond defensively if necessary. Because female fitness is dependent upon maintaining access to the resources required to successfully raise offspring, risk-averse females still benefit if the intergroup conflict is won. On the other hand, winning intergroup conflicts does not provide males with any significant resource-based benefit, and if they are likely to have vulnerable offspring, they may even prefer to avoid escalated intergroup conflicts altogether. Thus, the fitness-maximizing strategies of male and female group members are prone to conflict during many intergroup conflicts.

We further provide evidence that both males and females have evolved manipulative strategies to deal with this conflict of interest. Females use punishment and rewards to recruit male support when males are reluctant to assist in fighting for resources that are limiting to female fitness. Conversely, males who are likely to have sired offspring use punishment and coercion to inhibit females, as well as other group members, from

instigating or participating in intergroup aggression. Thus, females use social incentives to promote more effective group-level cooperation when the benefits for themselves are high, while males use social incentives to stifle group-level cooperation when the potential costs are significant. These results provide novel evidence that social incentives to effectively manipulate the participation of fellow group members during high-risk intergroup conflicts, are not uniquely human. Additionally, we have strived to understand why these manipulative strategies evolved in this study system, and we discuss the types of social systems and cooperative activities in which similar social incentives are likely to be found among other non-human animals.

ZUSAMMENFASSUNG

Gruppen bestehend aus sozialen Tieren sind typischerweise eine Ansammlung egoistischer Individuen, welche jeweils verschiedene Vor- und Nachteile aus dem Gruppenleben ziehen. Daraus resultieren verschiedene fitnessmaximierende Strategien für die einzelnen Gruppenmitglieder. Die Muster der kooperativen Verhalten, welche auf Gruppenlevel entstehen, können sehr dynamisch sein, abhängig von dem möglichen Gewinn und Risiko, welche mit der kooperativen Aktivität assoziiert sind, und den Interessenkonflikten zwischen einzelnen Gruppenmitgliedern. Zum Verständnis der evolutionären Mechanismen welche Kooperationsmuster steuern, ist es deshalb kritisch, die Faktoren zu verstehen, welche die individuellen Entscheidungen beeinflussen. Das Ziel dieser Dissertation war es, die Vielfältigkeit und das Zusammenspiel verschiedener fitnessmaximierender Strategien von Südlichen Grünmeerkatzen (*Chlorocebus aethiops pygerythrus*) im Kontext von kooperativen Zwischengruppen-Aggressionen zu verstehen.

Dazu haben wir die ressourcenbasierten Vorteile untersucht, welche die männlichen und weiblichen Grünmeerkatzen mit einer Teilnahme an den aggressiven Zwischengruppen-Konflikten gewinnen können. Zusätzlich haben wir die Interessenkonflikte, die zwischen den verschiedenen Gruppenmitgliedern entstehen, identifiziert und die manipulativen Strategien untersucht, welche die Männchen und Weibchen benutzen, um die Konflikte zu lösen und ein besseres Resultat für sich selbst zu erreichen.

Durch die Untersuchung der Variabilität der Teilnahme in den Zwischengruppen-Konflikten innerhalb eines Individuums und zwischen verschiedenen Individuen, konnten wir zeigen, dass Weibchen und Männchen aus unterschiedlichen ressourcenbasierten Gründen teilnehmen und verschiedene Strategien haben, um die Risiken der Konflikte zu reduzieren. Die Weibchen verteidigen den Zugang zu wertvollen Nahrungsressourcen und häufig genutzte Bereiche in ihrem Streifgebiet. Die Männchen hingegen verteidigen den Nachwuchs und unterstützen die Weibchen, wenn dies mit einer Erhöhung des Paarungserfolgs hereingeht (z.B. während der Paarungszeit). Das letztere Resultat hebt hervor, dass die Weibchen in der Lage sind ihre Paarungspartner selbst zu wählen, wobei sie Paarungsmöglichkeiten als Druckmittel verwenden, um sich die Kooperation der Männchen zu sichern. Männchen, sowie Weibchen, scheinen sich der Gefahr für ihren Nachwuchs während eskalierten Konflikten bewusst zu sein; während Weibchen mit Jungtieren dazu tendieren, die Frontline zu meiden, verharren potentielle Väter an der Frontline um den Verlauf der Begegnung zu überwachen und falls nötig verteidigend einzugreifen. Da die erfolgreiche Aufzucht des Nachwuchses für die Weibchen mit dem Zugang zu Ressourcen zusammenhängt, können selbst risikoscheue Weibchen profitieren, wenn der Zwischengruppen-Konflikt gewonnen wird. Andererseits erhalten die Männchen keinen wichtigen ressourcenbasierten Gewinn aus einem Sieg. Haben sie hingegen wehrlosen Nachwuchs, können die Männchen sogar vorziehen den Konflikt nicht eskalieren zu lassen. Die verschiedenen fitnessmaximierenden

Strategien der Männchen und Weibchen sind daher anfällig auf Konflikte während vielen Zwischengruppen-Konflikten.

Ausserdem konnten wir den Nachweis erbringen, dass Männchen und Weibchen manipulative Strategien evolviert haben, um mit diesem Interessenkonflikt umzugehen. Weibchen benutzen Bestrafung und Belohnung, um sich die Unterstützung von Männchen zuzusichern, wenn diese zögern, ihnen beim Kampf um fitnesslimitierende Ressourcen zu helfen. Männchen mit hoher Vaterschaftswahrscheinlichkeit dagegen greifen auf Bestrafung und Nötigung zurück, um Weibchen und andere Gruppenmitglieder von der Teilnahme an Zwischengruppen-Aggressionen abzuhalten. Somit benutzen Weibchen soziale Anreize um effektivere Kooperation auf Gruppenebene zu fördern, wenn ihr eigener Gewinn hoch ist. Männchen dagegen benutzen soziale Anreize zur Förderung der Kooperation auf Gruppenebene, wenn die potenziellen Kosten signifikant sind. Diese Resultate liefern neue Evidenz, dass soziale Anreize, welche benutzt werden um die Teilnahme von Gruppenmitgliedern während risikoreichen Zwischengruppen-Konflikten zu manipulieren, nicht nur von Menschen eingesetzt werden. Zusätzlich haben wir zu verstehen versucht, warum solche manipulativen Strategien in diesem Studiensystem entstanden sind, und wir diskutieren die Arten sozialer Systeme und kooperativer Aktivitäten, bei welchen der Einsatz von ähnlichen sozialen Anreizen in nicht-menschlichen Tieren gefunden werden könnten.

ACKNOWLEDGEMENTS

I would like to invite you to make a big mug of tea – or pour a large weizen, if you like your beverages a little bit zippier – grab a cozy blanket, and curl up by the fire as I have many acknowledgements to make. I absolutely love my PhD and I am very excited to officially thank everyone who made this entire experience possible, and all those who supported me along the way.

So, let us start with my amazing supervisors, Erik and Carel. I am not sure how I convinced you two that I was the girl for the job – maybe it was the itchy feet, or maybe it was because you thought I was a French guy – but I am very grateful to have been chosen. Your mentorship has been exceptional and I feel incredibly lucky that I got to be part of the van Schaik Dream Team for a few years. You guys taught me an incredible amount about monkeys, data collection, statistics, scientific writing, and evolutionary biology. You allowed me to chase the monkeys around for 2.5 years, collecting all the data my little heart desired, and then when I came home, you helped me understand the mechanisms behind all the cool behaviours I had observed in the field, and why these would have evolved. With your guidance, observations that likely would have been a couple of anecdotal paragraphs buried in my dissertation, were developed into two papers that I am super proud of. My dream is to make a career in academia, and I would like to think that my cherished mentors have gotten me much closer to this goal by moulding me into a significantly better scientist than I was when I arrived.

Erik, as my numero uno mentor, you must be given your own special thank you. I have so much respect for you and being your little grasshopper has been incredibly rewarding – wax on, wax off –. For the past six years, you have inspired me, pushed me, encouraged me, and always had my back. I will miss planning my fieldwork in *Acacias* and *Ficus'*, skipping down the hallway in my giraffe slippers to share my latest results, maximizing our brainstorming sessions by keeping you hopped up on gummy candy, early-Jean late-Erik skype sessions, and discussing how to make the next paper sexier. You gave me all the time and support that I asked for, gently worked on thickening up my skin, and you infused my PhD with happiness. I hope that you are as delighted to have had me for a student as I am to have had you as a supervisor, mentor and role model.

My PhD would not have been possible without the whole IVP team, and IVP started with Erica. Thank you, Erica, for your big dreams, for recruiting Andy, Redouan and Carel, for organizing the Synergia grant, for getting IVP up and running, for keeping it going, and for all the hard work and tenacity it took to turn the project into the unique field site that it has become. I would also like to thank all of the students and volunteers who toiled away under the hot African sun, working hard to habituate monkeys, collect behavioural data, keep up with your focals, scoop up poop samples, and estimate the number of fruits in the biggest *Ziziphus* trees. You guys made the project what it is, and I am infinitely grateful for all of your help. I will miss sitting around the dinner table and listening to you guys argue about which group is the coolest, which male is the sexiest, and which

females are the biggest bitches. I will miss dancing around the living room with you, sharing sunset Savannah's on the rooftop, stripping down and holding hands to cross the river, and the joy of rainy day pancakes. No two people are more a part of these happy memories, and have dedicated more of their lives to making IVP a success, than Chris and Stef. I am especially thankful to both of you.

One of the best parts of my PhD is that it brought two very lovely Swiss girls into my life. Anouk and Eliane both arrived in South Africa at times that I was feeling overwhelmed with fieldwork. Having you ladies to discuss problems with, brainstorm solutions, and rely on for help, made the stressful times manageable. You took on all tasks without complaint, whether they involved hours of trying to figure out what a tall open woodland was – the answer to which is still, I have no idea –, tediously updating the database forms, repeatedly gluing silk flowers onto jingle boxes, and being the leopard model, even when it involved crawling through cacti and laying in a ball on the ground for hours on end. You were also my first contact for discussions of monkey behaviour in the field; it was through our conversations that I became confident that the monkeys were using punishment. I owe you both so much for all this support whilst in Africa, and I will cherish many happy memories of our times together, but I am more grateful for your friendship. Your lessons on Swissification have had an enormous impact on my life, making me a happier and more balanced Jean. You will both always be my most cherished MSc students.

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In many ways, doing a PhD on monkey behaviour and trying to make it in academia, is a bad life decision, and a path you should only take if it makes you so happy that you cannot imagine doing anything else. I would not be pursuing such a dream without the support and encouragement of my family. My deepest gratitude to my mom, my gramma, to Dwight and Marylou, and to the most important person in my world, Nicholas. You have been amazingly supportive, even though following my dreams meant spending years on separate continents. I am grateful for all your Africa visits – our adventures on the dark continent will always be among my most

happy memories – as well as the side trips to Vietnam and to Switzerland. I also thank you for pretending to be interested every time I pulled out the white board so we could discuss the evolutionary mechanisms driving monkey behaviour, for allowing me to turn road trips into lessons on game theory – always a crowd pleaser – and for your countless hours spent editing papers. Most importantly, I want to thank you for always believing in me, reassuring me, boosting my confidence, and making me believe that I can do this. Lastly, I would like to thank our friend Matthew for being our dedicated third wheel. It was easier being abroad for so long, knowing that you were dragging Nicholas out for beers, to baseball games, and camping while I was gone.

GENERAL INTRODUCTION

Cooperation has played a critical role in the evolution of life's complexity, as it has been an important selective pressure in many of the major transitions in evolution (Smith and Szathmary 1997). It is through cooperation that alliances between individuals of the same, or different species, can produce new evolutionary agents. Cooperation is also a pervasive feature of group living. Although individuals who live in stable social groups must compete with group members for resources and reproductive opportunities, they also cooperate to raise and protect offspring, hunt, watch for and ward off predators, or defend access to fitness-limiting resources (Packer and Ruttan 1988; van Schaik 1983; van Schaik 1996; Wrangham 1980). Because larger groups tend to be able to outcompete conspecifics, intragroup competition is thought to have played a key role in driving the evolution of sociality (van Schaik 1983; van Schaik 1989; Wrangham and Rubenstein 1986; Wrangham 1980), as well as altruistic behaviour (Bowles 2006; Bowles 2009; Bowles 2012; Bowles and Gintis 2011). As such, cooperation is a principle that is particularly relevant to understanding hominin evolution (Bowles and Gintis 2011).

One of the most notable differences between humans and other animals is the extent to which we engage in cooperation; we help unrelated strangers we are unlikely to meet again, cooperate in high risk activities such as warfare, and cooperate effectively in large groups (Gat 2010; Melis and Semmann 2010; Silk and Boyd 2010). Throughout the latter stages of our evolutionary trajectory, intergroup conflict (i.e. war) has been a significant source of human mortality, and as a result, could have acted as a strong selective pressure for behaviours that enhance the competitive ability of the group (Bowles 2009). For example, selection may favour behaviours such as courage, sympathy and faithfulness, even though these behaviours increase the likelihood of death for individual warriors (Darwin 1896) Outside of humans, there is currently only limited empirical evidence that intergroup conflict influences intragroup cooperation (but see Bruintjes et al. 2015; Majolo et al. 2016; Radford 2008a; Radford 2008b; Radford 2011). Given the potential importance of intergroup conflict in shaping the evolution of social behaviour, understanding why individuals participate in this high-risk activity, the mechanisms promoting cooperation, and the fitness consequences of effective group-level cooperation is a highly relevant undertaking. Such investigations will provide insight into how we evolved our unique propensity to cooperate, and identify which aspects of our social behaviour are shared with, or distinct from, other animal species.

A number of evolutionary mechanisms could be important in promoting cooperation in a group setting (i.e. polyadic cooperation). For example, cooperative behaviours could be selected for if they increase the inclusive fitness of the actor (Hamilton 1964; Lehmann and Keller 2006; West et al. 2007), provide immediate benefits such that the behaviour is actually self-serving (i.e. by-product mutualism) (Brown 1983), trigger a self-serving

response in the receiver that has by-product benefits for the actor (i.e. pseudo-reciprocity) (Connor 1986), or have delayed benefits. Delayed benefits may be obtained if the receiver returns the investment in the future (i.e. direct reciprocity) (Trivers 1971), third party individuals return the investment in the future (i.e. indirect reciprocity or generalized reciprocity) (Nowak and Sigmund 1998; Pfeiffer et al. 2005), or if behaving cooperatively prevents others from using negative social incentives, such as punishment or policing (Clutton-Brock 2009; Clutton-Brock and Parker 1995; Ratnieks and Visscher 1989).

Because groups are a heterogeneous collection of individuals, each member gains different benefits, and experiences different costs from living, interacting, competing and cooperating with fellow group members. As a result, the patterns of cooperative behaviour that emerge at the group level can be highly dynamic, and context specific, depending on the identity of group members (e.g. their sex, age, size, experience, reproductive status), the benefits at stake, and the risks associated with the cooperative activity. It is therefore, critical to understand the factors influencing individual decisions when investigating group-level patterns of cooperation. Sex differences are a significant source of individual variability. There is typically an asymmetry in reproductive investment between the sexes, with females investing more time and effort into each reproductive event (Trivers 1972). Consequently, female fitness is primarily limited by the resources required to produce and raise offspring (Trivers 1972). Conversely, the scarcity of receptive females means that these are the resource most limiting to male fitness (Trivers 1972). As a result, males and females have different intrinsic interests, experience different selective pressures, evolve different fitness-maximizing strategies, and are likely to contribute to group-level cooperation under different conditions (Fashing 2001; Muller and Wrangham 2009; Smuts and Smuts 1993; Trivers 1972). That is, if the risk of injury does not inhibit them from participating in intergroup conflicts. When sexual dimorphism is large, members of the smaller sex may be unable to express their interests (Willems et al. 2013), and as a result, they may not exhibit strategies that would enhance their own fitness.

Intergroup aggression is one of the riskiest cooperative activities that social groups engage in, potentially resulting in injury or death (Cant et al. 2002; Cheney and Seyfarth 1987; Gros-Louis et al. 2003; Kruuk 1972; Mech 1994; Mosser and Packer 2009; Watts et al. 2006). Over the last few decades, there has been a flurry of work on intergroup competition, in a diverse array of species including insects, birds, carnivores, primates and humans (Boydston et al. 2001; Carlson 1986; Cheney 1981; Farabaugh et al. 1992; Glowacki and Wrangham 2015; Hölldobler 1981; Robbins and Sawyer 2007). Our understanding of why individual group members participate in intergroup conflicts has grown tremendously, and sex differences have been emphasized consistently (Boydston et al. 2001; Cheney 1981; Cheney 1987; Fashing 2001; Kinnaird 1992; Koch et al. 2016; Majolo et al. 2005; Zhao 1997). As predicted by sexual selection theory (Trivers 1972), females tend to fight for resources such as food and territory (Boydston et al. 2001; Fashing 2001; Kinnaird 1992; Nunn and Deaner

2004; Wich et al. 2002; Zhao 1997). Conversely, many studies have found that males defend access to mates (Cooper et al. 2004; Fashing 2001; Henzi et al. 1998; Kitchen et al. 2004; Koch et al. 2016; Majolo et al. 2005; Robbins and Sawyer 2007; van Schaik et al. 1992; Zhao 1997) or protect their offspring, although this strategy is most common in species that exhibit infanticide (Borries 1997; Grinnell et al. 1995; Kitchen 2004; Watts 1989; Wich et al. 2004). Offspring survivial, mates, food and territory could all be considered resources, and therefore, much of the work on intergroup conflicts in animals has focused on resource-based, or material, benefits.

In the human literature, there has been a greater focus on examining not just the resource-based benefits, but also the immaterial benefits gained from participating in cooperative intergroup aggression (i.e. primitive warfare) (Glowacki and Wrangham 2013). Resource-based benefits are obtained from seizing valuable items from neighbouring groups, such as food, captives, weapons and territory (Almagor 1979; Durham 1976; Eaton 2008; Gat 2000; Gat 2010; Glowacki and Wrangham 2013). Conversely, immaterial benefits are the social incentives that group members bestow on warriors (Glowacki and Wrangham 2013). For example, male warriors may receive gifts or improve their status with group members, and as a result enjoy increased access to allies or wives in the future (Chagnon 1988; Cronk 1991; Glowacki and Wrangham 2015; Glowacki and Wrangham 2013; Hill 1984; von Rueden et al. 2010). Warriors who do not fight, or exhibit cowardice, can be ostracized, shunned, ridiculed or punished (Dozier 1967; Mathew and Boyd 2011; Mathew and Boyd 2014; Meggitt and Meggitt 1977; Robbins 1982). Although these social incentives are often considered to be a more important motivator of primitive warfare, there is little evidence that non-human animals use social incentives to influence the participation of fellow group members during cooperative intergroup aggression. This absence of manipulative strategies is perhaps surprising, given the conflicts of interest that theoretically exist among group members, and the evidence supporting that indeed individuals differ greatly in their motivations to fight versus avoid high-risk intergroup conflicts. Do non-human animals only fight for resource-based benefits? Or are social incentives used but have yet to be uncovered?

Aim of Research

The overall goal of this doctoral dissertation was to develop a comprehensive understanding of cooperative intergroup aggression in vervet monkeys (*Chlorocebus aethiops pygerythrus*). To achieve this, we first investigated the sources of intra- and interindividual variability in participation in intergroup conflicts. These sources of variability allowed us to identify the different resource-based benefits that males and females fight for. Therefore, these investigations provide insight into the role that inclusive fitness benefits (e.g. offspring defence) play in motivating cooperative intergroup aggression, as well as the extent to which apparent cooperation is simply a by-product mutualism, with each partner participating to obtain resource-based

benefits. The patterns of intra- and interindividual variability in participation also shed light on how costly males and females each perceive participating in, or even experiencing intergroup conflicts to be. Thus, understanding intra- and interindividual variability allowed the conflicts of interest between the sexes to be elucidated. Second, we investigated whether female and male vervet monkeys use social incentives to deal with these conflicts of interest. To do so, we examined whether male and female intragroup aggression and grooming influence the participation of group members during intergroup conflicts, and tried to understand the social and ecological contexts in which these behaviours are used.

Study Site and Study Species

Data collection for this dissertation was conducted at the Mawana Game Reserve (28°00'S, 31°12'E), in South Africa. Here, the research team of the Inkawu Vervet Project, studies three fully habituated groups of vervet monkeys. The adults in most of the neighbouring groups are also individually recognized and two additional groups are habituated enough to allow for some data collection to take place, although the detailed life histories of these groups are not yet known.

Vervet monkeys live in multi-male multi-female groups in which females are the philopatric sex (Struhsaker 1967). Males disperse after reaching sexual maturity, and can disperse multiple times throughout their lives (Cheney and Seyfarth 1983). Sexual dimorphism is moderate, with males being approximately 1.5 times larger than females (Cheney 1981), and although they are smaller, females can aggress male group members and even outrank them (Struhsaker 1967). Vervet monkeys are seasonal breeders, females have concealed estrous, and they are highly promiscuous, mating with multiple males throughout the mating season (Andelman 1987). As a result, males are unable to monopolize receptive females, and are thought to have low paternity certainty (Andelman 1987). Not only do females mate promiscuously, but they are also able to refuse matings, indicating that they are able to exert a large amount of female choice (Keddy 1986). Given that females can dominate males and control male reproductive opportunities, female vervet monkeys likely have more leverage over males than is typical for most primates. Recent evidence suggests that females can even use this leverage to influence the dominance rank of preferred male group members, suggesting that males could benefit greatly from forming strong relationships with female group members (Young et al. 2017)

Previous work on vervet monkeys has found that intergroup interactions ranged from affiliative to highly aggressive, and that both males and females participate in intergroup conflicts (Cheney 1981). Although individual participation was highly variable, overall, high-ranking individuals were more likely to participate aggressively. However, in males, it was unclear if this was because they were those with priority of access to sexually receptive females or those with the most offspring in the group (Cheney 1981). The former could indicate that males fight to defend access to mates, while the latter could mean that males fight to protect

offspring. Males were also observed to direct aggression towards females of their own group during 20% of the observed intergroup conflicts (Cheney 1981). This behaviour has often been referred to as 'herding' and is thought to function to prevent females from fraternizing with, or mating with extra-group males (Cheney 1981; Cheney 1987). Conversely, females were thought to fight for access to food resources (Cheney 1987) and they often formed coalitions with close kin when participating in intergroup conflicts (Cheney and Seyfarth 1987). Although intergroup conflicts can involve contact aggression and males have been observed to wound females, only infants under a year old have been reported to die as a result of intergroup aggression (Cheney and Seyfarth 1987). While juvenile and subadults also participated aggressively, young males often affiliated with members of opposing groups during intergroup encounters; these affiliative interactions may inform future dispersal decisions and facilitate transfer between groups (Cheney 1981).

Outline of the Dissertation

Chapter 1 examines the causes of intra- and interindividual variability in female participation in intergroup conflicts. We find that the resource-based benefits that females fight for include both food resources and areas that are used intensely over the long-term. High-ranking females are more aggressive than low rankers suggesting that females modulate their participation according to their priority of access to defended resources. Females are less likely to participate in intergroup conflicts in years that they have infants, indicating that conflicts are perceived as risky to small offspring. Conversely, females are more active during intergroup conflicts in which males provide high levels of support, suggesting that females perceive intergroup aggression to be less risky when their larger male group members are also fighting. This chapter was published in Animal Behaviour in 2017.

In Chapter 2, we investigate the causes of intra- and interindividual variability in male intergroup aggression. By considering the context in which intergroup aggression was exhibited, we are able to identify different types of male participation. Males frequently respond reactively when the opposing group is aggressive, and this defensive aggression is used by males who are likely to have sired offspring, particularly when there are small infants in the group. Therefore, defensive aggression appears to function to protect offspring. Another type of aggression that is frequently exhibited by males is to support females who instigate intergroup aggression. Males exhibited this type of aggression during two seasons: the summer season, which is when high-quality food resources are abundant, and the mating season. Thus, there is some evidence suggesting that males may fight to defend food resources; however, males who frequently support female instigators during intergroup conflicts experience the highest mating success, suggesting that males may exhibit this type of aggression to improve their status with female group members. Chapter 2 was published in Animal Behaviour in 2015.

In Chapter 3, we use a novel experimental approach to further clarify the findings of Chapter 2, and better determine if male intergroup aggression functions to defend food resources on behalf of females, to advertise male quality, or to improve their status as a cooperative group member. We simulated the presence of a neighbouring group nearby, doing so both when female group members did versus did not have access to a high-quality food resource that we provided, and from which males were excluded. Males do not appear to defend food to increase the reproductive success of female group members because their response is not influenced by the presence of provisioning boxes that only females could access. However, focal males almost always followed/supported female group members who initiated an approach towards simulated intruders, supporting the idea that male participation largely functions to gain status as a cooperative group member. Therefore, the apparent evidence for male food defence found in Chapter 2, is more likely a by-product of intersexual cooperation. Chapter 3 was published in Scientific Reports in 2016.

In Chapter 4, we investigate whether female intragroup aggression and grooming, in the context of intergroup conflicts, potentially function as social incentives. We find that females selectively groom males that have recently participated in the intergroup conflict, but aggress male group members that have not. Males who receive either aggression or grooming subsequently participate above their personal base-line level. Therefore, female-male aggression and grooming appear to function as punishment and rewards (respectively), and effectively promote male participation in intergroup conflicts. Females use these manipulative tactics in the season when, and in areas of their home range where, high-quality food resources are most abundant, suggesting they use social incentives to recruit males when valuable food resources are at stake. Because the probability of winning intergroup conflicts is dependent on the relative number of active participants between the two groups, recruiting males may help females to increase access to the resources which limit their own fitness. This chapter was published in the Proceedings of the Royal Society B in 2016.

In Chapter 5, we examine the function of male intragroup aggression and grooming during intergroup conflicts. We find that male intragroup aggression is primarily directed towards individuals who have either just finished exhibiting, or are currently attempting to instigate intergroup aggression. Targeted females are less likely to instigate intergroup aggression in the future, indicating that male intragroup aggression functions as coercion (when directed towards those who are currently trying to instigate a conflict) and punishment (when directed towards those who have recently fought). These manipulative tactics effectively prevent intergroup encounters from escalating into conflicts. Males who are likely sires are those most likely to use punishment/coercion, particularly when they are wounded, and therefore less able to protect vulnerable offspring should a risky intergroup conflict erupt. This work, along with the findings in Chapter 4,

highlight the conflict of interest that exists between the sexes, as well as the role that social incentives can play in resolving this conflict.

CHAPTER 1

Intra- and interindividual differences in the costs and benefits of intergroup aggression in female vervet monkeys

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In social species, fighting in intergroup conflicts is one of the riskiest cooperative activities group members engage in, particularly for individuals of the smaller sex. In a number of species, female group members are significantly smaller than males and as a result, the costs associated with intergroup aggression outweigh the potential benefits, and females avoid participating. Studies conducted on species in which females are active participants have consistently found that they fight to defend access to food resources and that high-ranking females tend to be more active than low-rankers. However, additional factors may modulate the costs and benefits of participation, creating differences among individuals and variability within individuals over time. In this study, we investigate a number of costs and benefits that potentially affect female vervet monkey (*Chlorocebus aethiops pygerythrus*) participation in intergroup conflicts. We observed the participation of 35 females in three groups, during 115 intergroup conflicts. Our findings suggest that female vervet monkeys defend access to valuable food resources, as well as to areas that are intensely used in the long-term; however, rank also influenced female participation indicating that the potential benefits gained from resource defence vary with one's priority of access to these resources. We find that females were more likely to participate aggressively when they did not have an infant, and when they received more male support throughout the intergroup conflict, suggesting these factors influence the perceived risk, or costs, of intergroup aggression. Because we observed considerable temporal variability in both the proportion of female group members with infants, and the number and identity of male group members (i.e. amount of male support provided), the relative fighting ability of neighbouring groups will inevitably fluctuate. Thus, our findings may help explain the lack of stable intergroup dominance relationships observed in many studies of intergroup conflict.

Introduction

Intergroup conflicts are one of the riskiest cooperative acts in which social groups engage as they can potentially result in the injury, or even death of participants (Cant et al. 2002; Cheney and Seyfarth 1987; Fashing 2001; Goodall 1986; Hölldobler and Lumsden 1980; Mech 1994; Mills 1983; Mosser and Packer 2009). Even when the risk of injury is relatively low, intergroup conflicts can last for long periods and involve vigorous activities such as long chases (Sillero-Zubiri and Macdonald 1998; Sorato et al. 2015; Wich and Sterck 2007), and impose significant opportunity costs on participants (Mares et al. 2012). Individual group members must each weigh these costs against potential benefits and decide whether to participate or defect from cooperative intergroup aggression. Because male fitness is primarily limited by access to receptive females (Trivers 1972), it is thought that males mainly participate in intergroup conflicts to defend access to mates (Cooper et al. 2004; Fashing 2001; Kitchen and Cheney 2004; Koch et al. 2016; Majolo et al. 2005; Payne et al. 2003; Zhao 1997). Conversely, female fitness is most limited by access to the resources required to produce and raise offspring (Trivers 1972), and therefore, females are thought to participate in intergroup conflicts to defend access to resources such as territory, food, shelter and/or water (Boydston et al. 2001; Kinnaird 1992; Nunn and Deaner 2004; Zhao 1997). A number of other factors likely modify these basic costs and benefits;

however, few studies have specifically investigated how females decide whether to defect or participate in intergroup conflicts (Reviewed in Kitchen and Beehner 2007). In a number of social species, females are significantly smaller than males, making the risk of being injured during intergroup conflicts so great that they may not participate at all (Willems et al. 2013). As a result, female motivations for intergroup aggression are often not expressed and cannot be studied. Even in species where females do participate in intergroup conflicts, they are often less active than males (Reviewed in: Cheney 1987; Koch et al. 2016), making it difficult to obtain the data necessary to effectively examine the factors that influence intra- and interindividual variability in participation.

Although there is a risk of injury when two groups fight over contested resources, the level of risk may differ between groups, among individual group members, and depend on the behaviour of both fellow and opposing group members. An individual's reproductive status, age, size and fighting ability relative to the participants from the opposing group, can all affect how risky an intergroup conflict is perceived to be (Kitchen and Beehner 2007). For females, the level of sexual dimorphism and their reproductive status likely have a significant influence on risk perception. In species where sexual dimorphism exists, but is moderate enough that females are willing to participate in intergroup conflicts, females may perceive the risk of injury to be higher if males from the opposing group are likely to participate aggressively. Mothers have invested significant time and resources into each of their offspring, and infants are particularly vulnerable group members (Arseneau et al. 2015; Cheney and Seyfarth 1987; Hrdy 1974; Packer and Pusey 1983); thus, mothers could be expected to be risk averse during intergroup conflicts (van Schaik 1996).

In social species, competitive ability is typically thought to be a product of group size (Cheney 1987; Mosser and Packer 2009; Williams et al. 2004) and therefore, individuals in numerically inferior groups may be at a greater risk of injury (Hölldobler 1981; Mosser and Packer 2009; Sillero-Zubiri and Macdonald 1998). However, whenever cooperative intergroup aggression is not a collective but a joint action by a subset of group members only (Willems et al. 2015), the relative number of active participants, rather than relative total group size, may determine the outcome of intergroup conflicts (Zhao and Tan 2010) and the perceived risk of intergroup aggression. Furthermore, the identity of active group members may also influence individual decisions, with larger or more experienced fighters being more valued allies (Cassidy et al. 2015). For example, it is possible that for females, having support from larger male group members may mitigate the perceived risk of participation in intergroup conflicts. As a result, individuals may make instantaneous participation decisions based on the current activity of their fellow group members.

Females are predicted to fight in intergroup conflicts for access to limiting resources when resources are patchily distributed so as to be defensible (Sterck et al. 1997; van Schaik 1989; Wrangham 1980). However, when females reside in a stable home range, areas that consistently produce defensible resource may also be

valuable and females may defend these spaces, even when current resource availability is low. How females value space and food likely varies from species to species, depending on their diets, their local habitat, and the intensity of intergroup competition. The benefits gained from defending contested resources may also vary among individual group members, with high-ranking females, who have priority of access, experiencing the greatest incentive to participate in intergroup conflicts (Nunn and Deaner 2004; Payne et al. 2003; van Schaik 1989).

In this study, we investigated the costs and benefits of female intergroup aggression in vervet monkeys (*Chlorocebus aethiops pygerythrus*). Vervet monkeys live in multi-male multi-female groups and, although females are smaller than males, the level of sexual dimorphism is modest enough that females are willing to participate aggressively during intergroup conflicts (Cheney 1981). Females fight with and without male support, and can even physically attack members of opposing groups (Cheney and Seyfarth 1987). Although females direct intergroup aggression towards both males and females (Cheney 1981), their tendency to form a coalition when aggressing males during intragroup conflicts (Arseneau-Robar et al. 2016c), suggests that targeting males carries a relatively high risk of injury if the male retaliates. Therefore, the support of group members, and the support of larger-bodied male group members in particular, may mitigate the perceived risk of participation in intergroup conflicts. Vervet monkeys are a particularly suitable species for investigating intra- and interindividual variability in participation, as usually only a handful of group members are active in a given intergroup conflict, individual participation is highly variable, and larger groups are not guaranteed to win (Arseneau et al. 2015; Willems et al. 2015). As a result, individual decisions to defect or participate may have real consequences for the outcome of intergroup conflicts, subsequent resource access, and potentially the fitness of group members (Cheney and Seyfarth 1987; Lee and Hauser 1998).

The goal of this study is to examine the factors that influence female participation in intergroup conflicts, and thereby gain a better understanding of the costs and benefits of participation versus defection from cooperative intergroup aggression. We consider three factors which could potentially modulate the risk of injury, and thus the costs, associated with intergroup aggression: female reproductive status, relative group size and the amount of male support. We hypothesize that females with vulnerable infants will be more averse to the risks posed by intergroup conflicts and therefore, we expect that these mothers will avoid participating in intergroup conflicts. We also expect that having support from male group members mitigates the perceived risk of injury and therefore, that females will be more likely to participate when they have greater support from their larger-bodied male group members. Because individual participation is highly variable and only a handful of group members typically participate in a given intergroup conflict, we do not expect relative total group size to have a strong effect on the perceived risk of intergroup conflicts, and therefore we predict this variable will have a minimal impact on the likelihood that females exhibit intergroup aggression. Given the

prevalence of evidence for female food defence in the literature (Reviewed in Kitchen and Beehner 2007), we predict that females will be more likely to participate in intergroup conflicts that occur in the season when, and areas of their home range where food availability is greatest. However, because females are the philopatric sex, it is also possible that the long-term value of the intergroup conflict location (i.e. areas that are consistently used at a high intensity) could influence female participation. We further predict that high-ranking females, who have priority of access to food resources and therefore receive a disproportionate amount of the benefits of cooperative intergroup aggression, will be more likely to participate in intergroup conflicts.

Methods

Study Site, Study Subjects and Behavioural Data Collection

Data were collected on three habituated groups of vervet monkeys at the Mawana Game Reserve (28°00'S, 31°12'E), KwaZulu-Natal, South Africa, between January 2012 and February 2014. Three seasons are important in this species/population: the birth season, the summer season and the mating season (Arseneau et al. 2015). The birth season was indexed by the number of dependent infants (less than three months old) in the group; the first birth typically occurred in early October and the number of infants in the group peaked in late November to early December. Seasonal habitat productivity was indexed by the average NDVI for each month, and the summer season, when NDVI values were highest, typically peaked between December and April. The mating season typically ran from February or March, until August.

The study groups consisted of 30 to 56 individuals, six to 14 of which were adult females. All were individually recognized, as were most of the adults in four neighbouring and frequently encountered groups. Males were deemed adults when they dispersed from their natal group, while females were considered to be adults when they gave birth to their first infant. Individual females were classified as having an infant if they had an offspring that was less than a year old. We used the one year designation because although females likely perceive infants to be most vulnerable when they are very young and still clinging, many of the observed cases of attacks occurred when the infants were becoming more independent. It appears that this is when infants were more likely to stray too far away from their mothers to be quickly collected, and had also not yet learned where to flee to, if an intergroup conflict erupted. Infants left behind as their group fled the contested location were always attacked and in one case, the infant subsequently died. By the start of the next birth season (i.e. when infants are a year old) they seem to have learned which direction to flee when intergroup conflicts occur in the various areas of their home range.

Groups were followed for at least two full-day follows a week, for a total of >11 000 observation hours over the study period. During follow days, 10 minute group scans (Altmann 1974) were conducted every half

hour, during which observers recorded the location of the group center with a handheld GPS unit (Garmin GPSMAP64, Garmin Ltd.), and the behaviour of as many group members as possible. During follow days, intragroup social interactions were also recorded as all-occurrence data (Altmann 1974), and aggression and displacements were used to determine the dominance hierarchy. We re-calculated the dominance hierarchy each year so that female group members who had had their first infant (i.e. were deemed adults) could also be included. Hierarchies were estimated using both de Vries h' and the directional consistency index (DCI) because the de Vries method cannot determine a linear relationship when there are only a few individuals (i.e. less than 6), or provides inaccurately low linearity index values when interaction frequencies are low (Appleby 1983; Archie et al. 2006; Isbell and Young 2002; Isbell and Pruetz 1998; Koenig et al. 2004; Schmid and de Vries 2013), as was the case for mother-daughter dyads in this population. Both observed h' values and DCI values were significant in all but one case, indicating that female vervets in this population, as is well-established for this species (e.g. Struhsaker 1967), formed linear dominance hierarchies (h' range: 0.59 to 0.89; DCI range: 0.96 to 1). The one exception was in the smallest group (n = 6 females), where h' was 0.83 (p = 0.12) in the first year of the study period; however, the DCI indicated that the hierarchy was significantly linear. Therefore, we assigned individual females with a numeric value representing their ordinal rank, with "1" being the dominant female.

During follow days, whenever two groups approached within 100m of each other, observers noted the time and the location, and also began to record the participation of all adult female and adult male group members on an all-occurrence basis (Altmann 1974). Because the habitat at the study site is fairly open, and because individuals participating in intergroup conflicts tended to do so on the ground, it was possible to follow the front-line of the intergroup conflict and collect detailed behavioural data. Intergroup encounters were considered to be intergroup conflicts when one or more individuals from either group directed aggression towards the opposing group. Aggressive behaviours could be directed towards the opposing group as a whole (e.g., running at the group or making aggressive displays and/or vocalizations while in close proximity) or target specific individuals (e.g., chasing or biting). For each aggressive participation event, we recorded the identity of active individuals, behaviour(s) exhibited, and the identity of the target individuals (or their sex and age class when their identity was unknown). Individuals were deemed to have initiated the intergroup conflict if they were participants in the first aggressive event of the intergroup conflict. Note that only individuals from the group who exhibited intergroup aggression first could be classified as initiating the intergroup conflict.

Delineating Mapping Units

Because the Mawana Game Reserve is an amalgamation of a number of smaller farms that have been allowed to regenerate, and these farms varied in their use of the land, the study site is comprised of fairly discrete

habitat patches. Some areas have relatively tall trees and dense vegetation cover, others are open woodlands, and others are regenerating fields that contain dense thickets of early successional trees and shrubs. The boundaries of these habitat patches tend to be clear and identifiable by abrupt changes in vegetation density and composition. The landscape is further fragmented by a number of natural (e.g. rivers) and man-made (e.g. roads and fence-lines) linear features, creating a mosaic of discrete areas. The vervet monkeys in the study population also treated the landscape as being heterogeneous as group members spread out within one area to forage, rest and socialize. Then, when moving to the next area, group members typically grouped together to travel as a cohesive unit, and then again spread out to forage, rest and socialize once in the next habitat patch. Furthermore, when an intergroup conflict occurred, the winning group typically pursued the losing group until all of its members had left the contested area (but did not pursue them past the boundary of the distinct habitat patch). Therefore, we delineated the study area into mapping units which represented these discrete habitat patches, using a satellite image of the study site, the changes in the density and composition of the vegetation, linear features, and the behaviour of the monkeys themselves (Figure A1.1).

Intensity of Use of Mapping Units

Previous studies have shown that the location in which an intergroup conflict occurs can have a significant effect on the participation of individual group members, and the outcome of the intergroup conflict (Crofoot and Gilby 2012; Crofoot et al. 2008; Furrer et al. 2011; Markham et al. 2012; Roth and Cords 2016). In accounting for this potentially important location effect, we did not use the distance to home range center (Crofoot and Gilby 2012) because in this population, study groups did not have a single, centrally located core area. Instead, all study groups had multiple mapping units that were intensely used, which could occur both near the center or the edge of the home range. Therefore, we determined which mapping units were, and were not, consistently used at a high intensity over the long-term (i.e. in both years of the study period). We used locations collected during group scans to estimate utilization distributions for each group, each year (i.e. January 2012 to January 2013, and Febrary 2013 to February 2014), using the Brownian bridge movement model (Horne et al. 2007) as implemented by Buchin and colleagues (Buchin et al. 2012; Buchin et al. 2015). We calculated the average intensity of use for all cells within each mapping unit for the first, as well as the second year of the study period. All groups had one or two mapping units that were consistently used at a high intensity (i.e. units that had a high long-term value), while the majority of mapping units within each groups' home range were not consistently used at a high intensity (>60% as often as the most intensely used mapping unit).

Habitat Productivity and Relative Food Availability among Mapping Units

We examined variability in habitat productivity both seasonally and spatially. Seasonal habitat productivity was indexed by monthly Normalized Difference Vegetation Index (NDVI) values from the MODIS MCD43A4 dataset (version 5, processed by NASA's LP DAAC (NASA Land Processes Distributed Active Archive Center (LP DAAC) 2014) and redistributed by WAMIS at: http://wamis.meraka.org/za/). The NDVI is a well-established proxy of the amount and vigor of green vegetation which correlates with the availability of food and shelter in vervet monkeys (Willems et al. 2009). High NDVI values were observed in the summer months (December to April), which is the period when almost all of the tree species important in the diet of the vervet monkeys in this population produce fruits. Conversely, outside of the summer season, the monkeys had a more varied diet, foraging for insects, eating tree sap, and sifting through the soil to find *Acacia* seeds that had dropped to the ground as the pods dried and cracked open.

While we used the intensity of use of each mapping unit to represent its long-term (i.e. annual) value to each group, the relative availability of food was used to represent the short-term (i.e. current monthly) value of each mapping unit. Within each month, we accounted for the spatial variability in food resources by determining the relative calories available from fruits in each mapping unit within each home range. Throughout the study period we conducted monthly phenology sampling, estimating the number of fruits per tree on 10 trees of each of the 9 species most commonly consumed by vervet monkeys at the field site (≥75% of their diet, based on the fruits consumed during group scans). We determined the spatial distribution of these species by overlaying the study area with a 100 m by 100 m grid and counting the number of trees of each species within each grid cell. We selected the four species that were most important in the diet of the study groups (~40% of their diet) and were also heterogeneously distributed. Using the caloric values of these fruits (Barrett 2009; El Ayadi et al. 2012; Feedipedia 2015) and the average number of fruits per tree observed during phenology sampling, we estimated the total calories available per grid cell, for each month of the study period. The calories per grid cell were averaged within each mapping unit, and we calculated the relative value of each mapping unit within each group's home range in a given month by dividing the average caloric value of each mapping unit by the average caloric value of the best unit available to that group, that month. Because we calculated the relative food availability of mapping units, we only included the tree species that were heterogeneously distributed, and therefore, whose availability varied among mapping units.

Statistical Analyses

We built two generalized linear mixed models (GLMMs). The first model tested which factors influenced whether or not individual females initiated intergroup conflicts, while the second model tested which factors influenced their propensity to participate throughout the intergroup conflicts. Predictor variables included

female rank and whether or not they had an infant, the three seasons (i.e. birth, summer and mating seasons), and the two location factors: the long-term intensity of use (low versus high) of the mapping unit the intergroup encounter occurred in, and the current availability of food in the contested mapping unit, relative to the rest of the home range. Additionally, because previous studies have shown that an individual's participation can vary with the relative fighting ability of its group (Heinsohn and Packer 1995; Kitchen 2006), we also added relative group size (number of adults and subadults in the focal group minus the number in the opposing group) as a predictor variable. In the second GLMM, in which we investigated female participation in intergroup conflicts, we also included the amount of male support that was given during the intergroup conflict as a predictor variable. The amount of male support was calculated as the proportion of aggressive events in the intergroup conflict, in which one or more males participated.

All statistical analyses were conducted in R (version 3.0.3, R Core Team 2014) using the lme4 (version 1.1-4, Bates et al. 2015), MuMIn (version 1.10.5, Bartoń 2014), and compete packages (version 0.1, Curley 2016). Because the response variable in both GLMMs was binary (i.e. initiate intergroup conflict yes/no, or participate in intergroup conflict yes/no), we set a binomial error structure and logit link function in our models. We included female identity nested within group, and intergroup conflict as crossed random effects to account for repeated sampling of individuals over different encounters (Zuur et al. 2009). We tested the significance of any interaction term that we thought biologically relevant using a likelihood ratio test (χ^2 test statistic), comparing the model with only main effects included, to the model with each interaction included (Bolker et al. 2009; Zuur et al. 2009). Only interactions that improved model fit at the significance level of $\alpha = 0.05$ were retained in the final model.

We based our inferences on full models plus important interaction effects rather than using a stepwise procedure (Forstmeier and Schielzeth 2011), and we did not interpret main effects if the predictor variable featured in a significant interaction effect. The significance of each GLMM was assessed by using a likelihood ratio test to compare the final model to the null model, which only included the intercept and random effects. The total variance explained ($R^2_{GLMM(c)}$) by each GLMM was estimated following the method described by Nakagawa and Schielzeth (Nakagawa and Schielzeth 2013).

Ethical Note

All data collection protocols were approved by the Ezemvelo KZN Wildlife board in South Africa.

Results

In total, we observed more than 400 intergroup encounters, half of which escalated into an intergroup conflict. We restricted our analyses to a subset of 115 intergroup conflicts in which all independent factors were known. There was a high amount of intra- and interindividual variability in the proportion of intergroup conflicts that the 35 females in the three study groups participated in (Figure 1.1). Some females were relatively consistent participants, some were almost never active, but most exhibited considerable annual variability in the proportion of intergroup conflicts that they participated in (Figure 1.1). In general, dominant females were frequently active in intergroup conflicts, whereas females who consistently defected from participating in intergroup conflicts tended to be low ranking. Additional variability may be attributed to reproductive status; when considering only those females that experienced annual variability in their reproductive status, we found that females participated in 35% of intergroup conflicts in year(s) that they did not have infants, and 23% of intergroup conflicts in year(s) that they did. The proportion of female group members to give birth in a given year ranged from 25% to 100%.

In our first analysis, we investigated the factors that influenced the propensity for individual females to escalate intergroup encounters into intergroup conflicts (i.e. participate in the first act of intergroup aggression). We found that high-ranking females were more likely to initiate intergroup conflicts than the lower-ranking members of their group (Table 1.1), and that alpha females were particularly likely to do so; they initiated approximately half of intergroup conflicts they experienced, while the average lower-ranking female only did so in 22% of the intergroup conflicts that they experienced. We also found that females were more likely to initiate intergroup conflicts when the contested location was within one of the mapping units that their group consistently used intensely over the long-term (Table 1.1).

In our second analysis, we investigated which factors influenced female participation throughout escalated intergroup conflicts. In general, females were more active in intergroup conflicts in the summer season when high-quality fruits were abundant, and high-ranking females were more active than low-ranking females **(**Figure 1.2**;** Table 1.2). However, rank effects were more pronounced when the intergroup conflict took place in mapping units that had high food availability, relative to the rest of the home range **(**Figure 1.2; Table 1.2). Rank effects were weaker when intergroup conflicts took place in mapping units with relatively little food available, but females still fought to defend these areas in the summer months when even areas with relatively low food availability contained valuable fruit resources (Figure 1.2; Table 1.2). We also found that females were more likely to participate in intergroup conflicts that occurred in mapping units that their group used intensely in the long-term (Table 1.2).

Having an infant had a strong negative effect on the propensity of females to participate during intergroup conflicts, indicating that females were significantly less likely to participate in intergroup aggression in years

that they gave birth than in years that they did not (Table 1.2). Conversely, females were more likely to participate aggressively during intergroup conflicts in which male group members provided high levels of support (Table 1.2).

Discussion

The aim of this study was to determine how various costs and benefits influence female participation during intergroup conflicts in a wild population of vervet monkeys. Overall, we found that females were more likely to participate in intergroup conflicts that occurred in areas that were used at a high intensity over the long-term, as well as in seasons when, and in areas of their home range where high-quality food resources were most abundant at the time. These findings suggest that female vervet monkeys defend access to current food resources, as well as areas that their group consistently uses at a high intensity, regardless of present food availability. However, the important effect that rank had on the propensity for females to initiate and participate throughout intergroup conflicts, indicates that the benefits gained from defending these resources varied with position in the dominance hierarchy, and therefore priority of access to the defended resources (Nunn and Deaner 2004; Payne et al. 2003; van Schaik 1989; Willems and van Schaik 2015).

We found that females were less likely to participate in intergroup conflicts in years when they had infants, but more likely to participate when male group members were also participating aggressively throughout the intergroup conflict. These findings suggest that the perceived risk of injury, or costs of fighting, varied with female reproductive status and the behaviour of their larger-bodied male group members. Many studies have assumed that females with infants should be less likely to participate in high-risk intergroup conflicts (e.g. Crofoot and Gilby 2012; van Schaik 1996), but few studies have actually tested this assumption (Cords 2007; Koch et al. 2016). We demonstrate that female vervet monkeys decrease their level of activity during intergroup conflicts when they have an infant. As has also been reported previously (Cheney and Seyfarth 1987), we observed infants being attacked by members of the opposing group. These attacks could result in death, indicating that intergroup conflicts can have very real fitness costs for females with infants, and may lead to risk-averse behaviour. Risk-averse behaviour was also evident among males who were likely to have sired offspring, as they tended to refrain from escalating intergroup aggression, and instead responded reactively when the opposing group was being aggressive (Arseneau et al. 2015).

Our finding that females were more likely to participate in intergroup conflicts when male group members provided high levels of support suggests that the perceived risk of injury associated with intergroup aggression is diminished when male group members also participate aggressively. Male vervet monkeys are approximately 1.5 times larger than females and have bigger canines, which likely makes them more valuable allies than group members of other age-sex classes. Females even use aggression as a punishment for non-

participation, and this manipulative tactic effectively recruits male support in fighting for high-quality food resources (Arseneau-Robar et al. 2016c). The value of consistent male support is further evidenced by the observation that when groups contained a male group member who was consistently highly aggressive during intergroup conflicts, members of opposing groups usually made no attempt to fight for the contested location (unless it was within one of their own intensely used mapping units), but simply fled. As a result, intergroup conflicts were brief, and therefore held a low opportunity cost when compared to encounters in later time periods (i.e. after this highly aggressive male emigrated), which could last for up to eight hours. Thus, males who consistently participate aggressively in intergroup conflicts may function much the same as 'impact hunters' (Gilby et al. 2015), reducing the perceived risk of injury for their female group members, and subsequently have a strong influence on the competitive ability of their group.

Classic sexual selection theory predicts that females should participate in intergroup conflicts primarily to defend access to food resources, and our findings support that this is the case in vervet monkeys. However, we also find evidence that females defend valuable space. Females both initiated, and were active throughout intergroup conflicts that occurred in mapping units that were consistently used intensely over the long-term. These highly valued areas did produce abundant resources at some point each year, but were fought for, regardless of present food availability. These intensely used mapping units likely contain other valuable resources, such as sleeping sites, but so did other mapping units which were not consistently defended. Alternatively, it is likely that as the philopatric sex, females know from experience which mapping units within their home range are the most productive and also provide access to other important resources (e.g. sleeping sites and water). That females were more likely to initiate intergroup conflicts when in these intensely used areas suggests that females consistently tried to defend access to these areas, even if they were not always successful. Consistently defending these valuable areas may help establish ownership of them by negatively conditioning neighbouring groups at those locations. Although focal groups did not enjoy exclusive access to these valuable mapping units, neighbouring groups used these areas at a low intensity, suggesting avoidance. Thus, consistent intergroup aggression in intensely used areas may simultaneously limit scramble competition and avoid actual contests in the future.

In social species, competitive ability is typically thought to increase with group size (Mosser and Packer 2009; Williams et al. 2004) but a number of studies have shown that smaller groups frequently win intergroup conflicts (Bonanni et al. 2010; Crofoot et al. 2008; Kinnaird 1992; Robinson 1988; Sugiura et al. 2000; Zhao and Tan 2010). When individual participation is highly variable, larger groups can suffer defeat if defection among group members is high (Crofoot and Gilby 2012; Crofoot et al. 2008). Therefore, the decisions of individual group members, and subsequently the relative number of active participants may determine the winner of intergroup conflicts (Zhao and Tan 2010). Given that females usually outnumber males in vervet groups,

female decisions to participate versus defect should have a disproportionate effect on the relative fighting ability of a group. We observed considerable annual variability in birth rates, and therefore, groups likely experience significant annual variability in their ability to win intergroup conflicts, being a more competitive group in years when few female group members give birth and the number of risk-averse mothers is small. However, the potential for male intergroup aggression to elicit the participation of multiple female group members, suggests that the decisions of individual males can have a disproportionate effect on the competitive ability of the group. The observed intra- and interindividual variability in the participation of males (Arseneau et al. 2015) indicates that temporal variability in group competitive ability is likely further exaggerated by changes in the composition and identity of male group members.

Although the amount of female support provided (i.e. intra-sexual cooperation) likely also influences female intergroup aggression, we were unable to examine to test its importance in this study, as it was impossible to determine if females were fighting together because they had a shared interest in defending resources, or because they were cooperating with their female group members. Future work is needed to determine the extent to which intra- and interindividual variability in participation, as well as the effectiveness of both intra- and inter-sexual cooperation, impact group competitive ability. However, our findings, and those from previous work in this population (Arseneau et al. 2015; Willems et al. 2015), highlight that social groups are complex entities whose members each experience a unique set of costs and benefits in participating in cooperative intergroup aggression, and as a result, intra- and interindividual variability is often significant. Temporal changes in group composition, and the reproductive status of male and female group members, likely have very real consequences for the number of active participants, and thereby impact group competitive ability. This flexibility in competitive ability may help explain the absence of stable intergroup dominance relationships in a number of social species, and the persistence of relatively small groups (Crofoot et al. 2008; Perry 1996; Robinson 1988; Sugiura et al. 2000). Such findings improve our understanding of the extent to which intergroup competition exerts selective pressure on the evolution and maintenance of sociality (Bowles 2009; Lehmann and Keller 2006; van Schaik 1983; West et al. 2007; Wilson and Wilson 2007; Wrangham 1980).

Chapter 1 Tables

Table 1.1 Factors affecting the probability that individual female vervet monkeys participated in the first act of intergroup aggression (i.e. initiated aggressive intergroup conflicts).

Fixed Effects	***b***	**SE**	***z***	***p***
(Intercept)	-3.15	2.34	-	-
Female characteristics				
Rank	**-0.31**	**0.08**	**-4.04**	**<0.001**
Had an infant that year	-0.41	0.56	-0.74	0.458
Seasonal factors				
Birth season	0.11	0.18	0.59	0.554
Seasonal habitat productivity (NDVI)	-2.55	3.84	-0.67	0.506
Mating season	0.58	1.27	0.45	0.651
Location factors				
Intensity of use of mapping unit	**3.85**	**1.13**	**3.40**	**<0.001**
Relative food availability in mapping unit	-0.02	0.02	-0.71	0.479
Relative group size	0.14	0.13	1.00	0.316

The final model was significantly different from the null model containing only individual nested within group, and intergroup conflict, as crossed random effects (likelihood ratio test: $n = 786$, $\chi^2 = 26.47$, $p < 0.001$, $R^2_{GLMM(c)} = 0.77$). Significant predictors are presented in bold.

Table 1.2 Factors affecting the probability that individual female vervet monkeys participated aggressively during intergroup conflicts.

Fixed Effects	***b***	**SE**	***z***	***p***
(Intercept)	-9.40	6.35	-	-
Female characteristics				
Rank	-4.32	1.31	-	-
Had an infant	**-1.74**	**0.58**	**-3.03**	**0.002**
Seasonal factors				
Birth season	0.13	0.23	0.58	0.560
Seasonal habitat productivity (NDVI)	15.03	13.10	-	-
Mating season	2.57	1.59	1.62	0.105
Location factors				
Intensity of use of mapping unit	**3.30**	**1.41**	**2.35**	**0.019**
Relative food availability in mapping unit	9.68	9.47	**-**	**-**
Relative group size	0.24	0.16	1.49	0.137
Amount of male support during intergroup conflict	**3.34**	**1.62**	**2.06**	**0.039**
Interactions				
Rank * Seasonal habitat productivity * Relative food	**-8.22**	**3.11**	**-2.65**	**0.008**

The final model was significantly different from the null model containing only individual nested within group, and intergroup encounter identity, as crossed random effects (likelihood ratio test: $n = 786$, $\chi^2 = 70.65$, $p < 0.001$, $R^2_{GLMM(c)} = 0.93$). Significant predictors and interactions are presented in bold.

Chapter 1 Figures

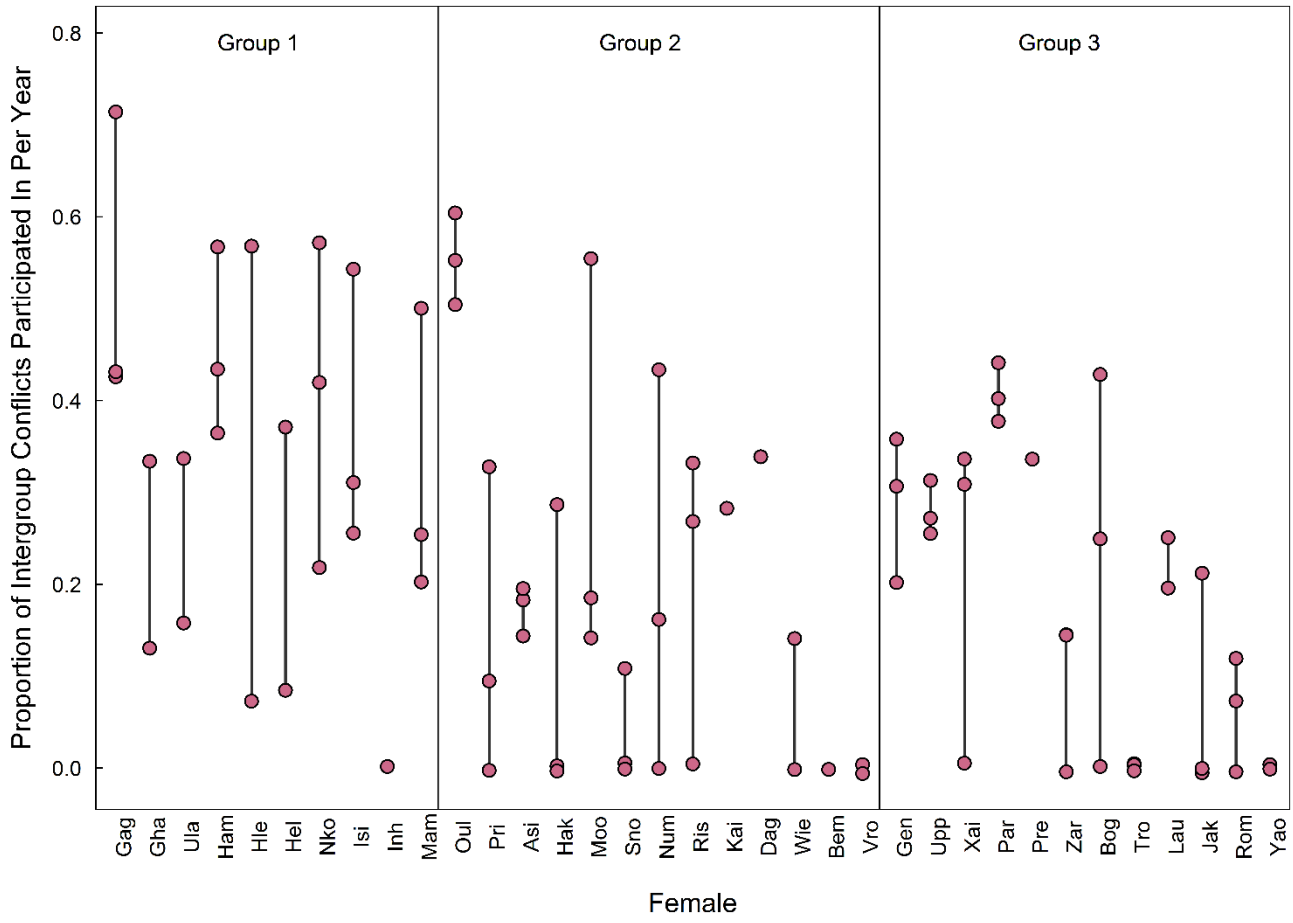

Figure 1.1 Annual variability in the proportion of intergroup conflicts experienced, that individual females participated in. Females are listed in order of descending rank, with the dominant female from each of the three groups listed first. Each dot represents a year of the study period; not all females were present in all years, and some females only reached adulthood in the second or third year of the study period.

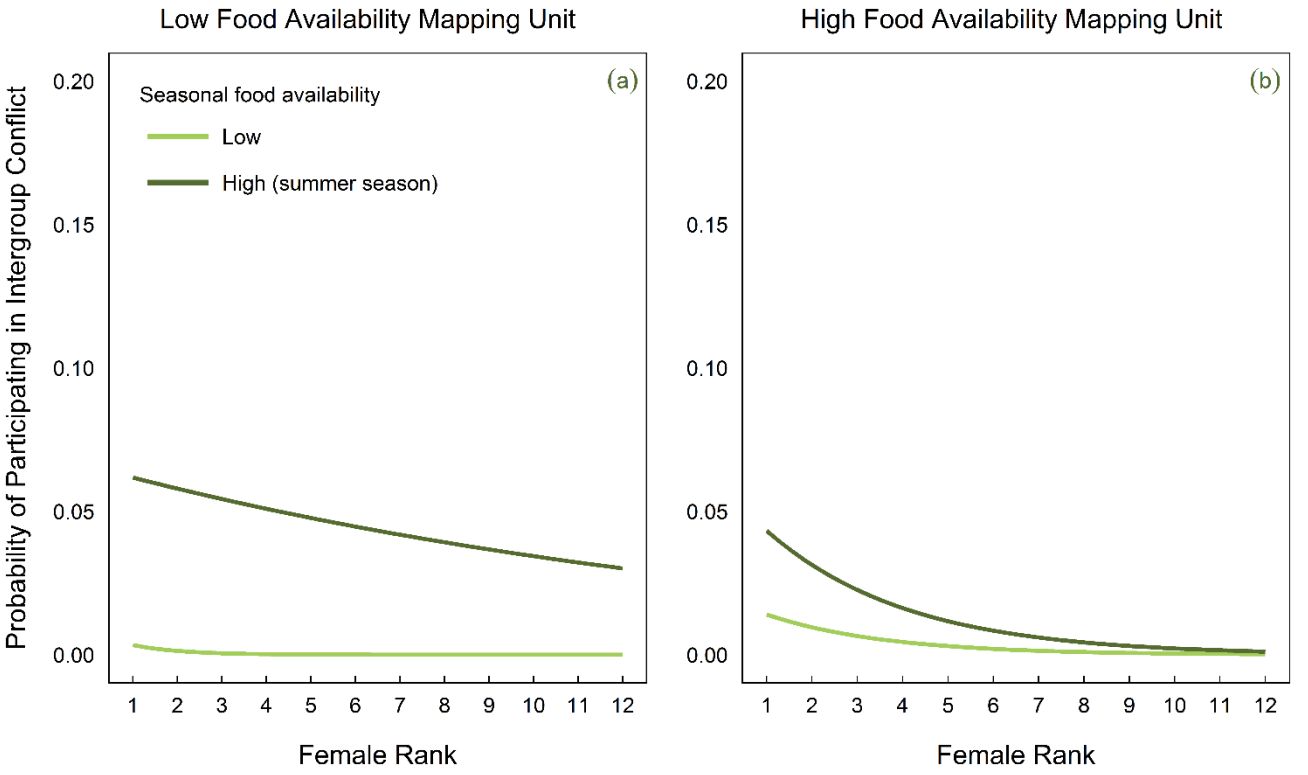

Figure 1.2 The probability that females participated aggressively during intergroup conflicts as a function of the 3-way interaction between dominance rank (with "1" being the dominant female), seasonal resource availability, and the relative availability of food within the contested mapping unit (compared to the rest of the home range). Prediction lines were obtained by plotting GLMM predictions (Table 1.2), setting all predictor variables not in the interaction term, to their mean values when the variable was continuous, or median values when the variable was binary. For visualization purposes, we set NDVI values to be above (dotted line) versus below average (solid line) to illustrate the effect that seasonal resource availability had on female participation. Similarly, we set the relative food availability to a low value (a) and to a high value (b) to illustrate the effect that the spatial distribution of food had on female intergroup aggression.

Chapter 1 Appendix

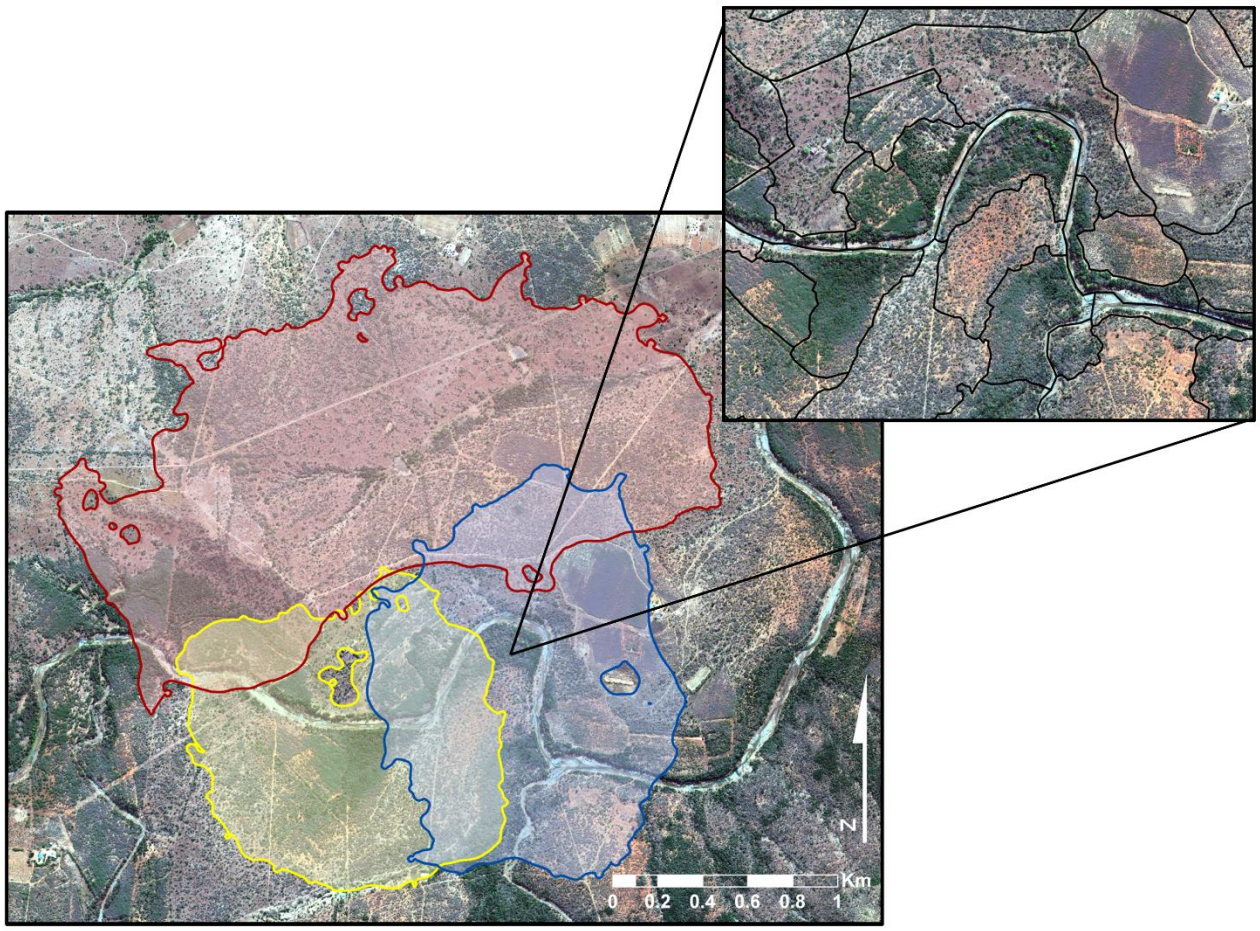

Figure A1.1 Map of the study area showing the three main study groups (yellow, red and blue polygons) and the mapping units (black lines) whose boundaries were delineated using abrupt changes in the vegetation density and composition, linear features (e.g. roads, fence-lines, or the river), and the behaviour of the monkeys themselves.

CHAPTER 2

Male monkeys fight in intergroup conflicts as protective parents and reluctant recruits

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In many social species, group members cooperate to defend a communal home range. Fighting in intergroup conflicts carries an opportunity cost, a risk of injury or death, and the possibility of exploitation by free-riding group members. As a result, it is rare that all group members fight in a given intergroup conflict, and individual participation is often highly variable. Thus, to understand the patterns of behaviour observed at the group level, we must first understand the causes of intra- and interindividual variability. Although sex differences have been well studied, our understanding of the relative importance of the various mechanisms promoting intergroup aggression within a sex is limited. We observed the participation of 22 male vervet monkeys, *Chlorocebus aethiops pygerythrus*, in 126 intergroup conflicts, and then partitioned aggressive acts according to the context in which they occurred. Using this approach, we found evidence that two mechanisms drive male intergroup aggression and, therefore, that individual variability is in part driven by the multiple selective benefits of participation. First, males that were likely to have sired offspring tended to exhibit defensive aggression and were more active when small infants were present in the group, suggesting they fight to defend probable offspring. Second, males were more likely to support females in initiating intergroup aggression just prior to, and during, the mating season. Female vervet monkeys are able to exert female choice and males that frequently supported female instigators tended to enjoy the highest mating success. These results indicate that males probably use intergroup aggression to improve their status with choosy females and subsequently maximize their mating success. Our findings indicate that a greater understanding of the evolutionary mechanisms promoting cooperative home range defence can be gained if we consider the context in which acts of intergroup aggression occur.

Introduction

In a diverse array of social species, group members cooperate during intergroup conflicts to defend access to space, mating opportunities, offspring or limiting resources such as food, water and shelter (Boydston et al. 2001; Hölldobler 1981; Manson et al. 1991; Mares et al. 2012; Mosser and Packer 2009; Wrangham 1980). Fighting in intergroup conflicts is costly because participation carries an opportunity cost, a risk of injury or death, and a risk of being exploited by free-riding group members (Nunn and Lewis 2001). Cooperative intergroup aggression creates a public good, where all group members benefit from the access to defended resources regardless of whether they contributed or not. Because individuals that do not participate gain the greatest net benefits, selection favours a cheating strategy, and cooperative intergroup aggression suffers from a collective action problem (Nunn and Lewis 2001; Olson 1965; Willems et al. 2013). This problem is avoided when group members are highly related and therefore can gain indirect fitness benefits from cooperating with group members (Nunn and Lewis 2001), as in cooperative breeders and eusocial insects. However, even in species in which participation in intergroup conflicts appears to be collective, individual participation is often highly variable and it is rare that all group members are active (Bonanni et al. 2010; Boydston et al. 2001; Carlson 1986; Heinsohn and Packer 1995; Kitchen 2006; Nunn and Deaner 2004; Zhao and Tan 2010). Thus, it is often the case that intergroup aggression is not truly a collective action involving all

members of a social group, but is rather a 'joint action' by a subset of individuals (Willems and van Schaik 2015). When action is joint, we should not regard social groups as monolithic units, but instead as complex systems composed of selfish entities (Arrow et al. 2000). The patterns of cooperative behaviour observed at the group level are an emergent property, which arise because of the individual benefits gained through participation and the social incentives exchanged among group members.

Individual benefits are gained in the process of producing the public good; conversely, social incentives are benefits that are bestowed on cooperative individuals by their fellow group members (Figure 2.1). Cooperative individuals may gain individual benefits when they have priority of access to the public good or when group members are close kin. In the context of intergroup conflicts, high-ranking individuals may gain asymmetric benefits and therefore be more likely to participate than other group members (Altmann 1962). Participants may gain inclusive fitness benefits via kin selection (Hamilton 1964), or intergroup aggression may serve to protect close relatives. Social incentives can be used to directly manipulate group members into cooperating (Clutton-Brock 2009; Clutton-Brock and Parker 1995; Glowacki and Wrangham 2013), or indirectly benefit those who participate in cooperative intergroup aggression by advertising their quality or improving their status with fellow group members. Potential indirect social incentive mechanisms include social prestige, reciprocity or indirect reciprocity (Alexander 1987; Trivers 1971; Zahavi 1975). The social prestige hypothesis predicts that participation in intergroup conflicts functions as an honest and costly signal of genetic quality, and that females who choose to mate with the best fighters ensure their offspring will have his superior genes (Zahavi 1975). The social prestige hypothesis is only feasible when females are able to exert female choice, such that males compete with each other to impress choosy females; this may be the case in multi-male groups, or when females are able to transfer between groups in order to access preferred males. Alternatively, individuals may engage in cooperative activities to make themselves a more valued group member with their cooperative partners (i.e. reciprocity) and/or with other group members who witness their cooperative behaviour (i.e. indirect reciprocity) (Alexander 1987; Axelrod and Hamilton 1981; Nowak and Sigmund 1998; Trivers 1971). Cooperative intergroup aggression could be used to build such status with potential coalition partners or potential mates, and a number of services could be exchanged (e.g. tolerance, grooming, support in agonistic interactions, food sharing and sex) (Borgeaud and Bshary 2015; de Waal 1997; Gumert 2007; Koyama et al. 2006; Seyfarth and Cheney 1984; Tiddi et al. 2011; Ventura et al. 2006); however, when females are able to exert female choice, mating opportunities are the most valuable commodity they have to trade with males. Determining the relative importance of these various individual benefits and social incentives in driving participation in intergroup conflicts will provide new insights into a major question in behavioural ecology: given the selective benefits of cheating, how could cooperation evolve, and how is it maintained?

In this paper, we focus on identifying the mechanisms driving male participation in intergroup conflicts in wild vervet monkeys, *Chlorocebus aethiops pygerythrus*. Vervet monkeys live in multi-male multi-female groups and members of both sexes are active in intergroup conflicts. Although females are smaller than males, both sexes can instigate intergroup aggression and, in rare cases, physically attack members of opposing groups. Vervet monkeys are a highly suitable species for investigating individual variability in intergroup aggression as usually only a handful of group members are active in a given intergroup conflict, and participation is highly variable both within and between individuals. Male intergroup aggression is particularly interesting because males may gain a variety of selective benefits from it (Fashing 2001). Males are the dispersing sex in vervet monkeys, and, as a result, kinship benefits are more likely through parental care than kin selection (Figure 2.1). Although offspring defence has primarily been seen in species that exhibit infanticide (Grinnell et al. 1995; Kitchen 2004), intergroup conflicts can result in infant mortality in this species (Cheney and Seyfarth 1987), which indicates that offspring defence could provide fitness benefits to males. Because male fitness is limited by access to receptive females (Trivers 1972), and male vervet monkeys often try to prevent immigration of other males, mate defence may be an important individual benefit (Cheney 1981). If so, then males with priority of access to mating opportunities (e.g. high-ranking males) should be more likely to exhibit intergroup aggression (Cooper et al. 2004; Kitchen 2004). If males, in defending mates, also end up defending food resources as a by-product, they are said to act as 'Hired Guns' (Fashing 2001; Wrangham and Rubenstein 1986). Males may also directly defend food resources to increase the reproductive output of their mates (Williams et al. 2004), a potentially beneficial strategy since resource availability has been linked to infant survival in vervet monkeys (Cheney and Seyfarth 1987; Lee and Hauser 1998). Alternatively, males may use intergroup aggression to obtain social incentives from their group members. Because male vervet monkeys do not form coalitions, we do not expect males to use intergroup aggression as a means to improve their status with potential coalition partners. However, moderate sexual dimorphism, female choice and the presence of multiple males in a group (Andelman 1987; Struhsaker 1967), indicate that males may participate in intergroup conflicts to signal their genetic quality to choosy females, or cooperate with females in exchange for other services such as mating opportunities. We are unaware of any non-human studies showing that rewards and/or punishment are used to manipulate participation in intergroup conflicts.

The aim of this study was to identify the causes of intra- and interindividual variability in intergroup aggression, in order to determine the relative importance of the various mechanisms driving male participation in intergroup conflicts. Although many studies have identified variation in the benefits gained by males and females (Fashing 2001; Kitchen 2004; Kitchen 2006; Van Belle 2015; Van Belle et al. 2014), uncovering variability in the selective benefits promoting intergroup aggression within and between individuals of the same age–sex class has proven more difficult. We are unaware of any studies that show clear evidence that multiple mechanisms are at work within a sex. This lack of evidence may be because only a single selective

benefit motivates individuals in many species, or because a different methodological approach is necessary to detect variability when it does exist. Previous studies have typically analysed whether individuals have, or have not, exhibited aggression during intergroup conflicts (e.g., Cooper et al. 2004; Fashing 2001; Harris 2010). However, there may be several acts of intergroup aggression within a single intergroup conflict, and because such an approach pools all of these, it inherently treats these independent acts as a homogeneous phenomenon. Doing so may mask intra- and interindividual variability in the selective benefits of intergroup aggression. Alternatively, if intra- or interindividual variability does exist, then acts of intergroup aggression may be motivated by different selective benefits, and the context surrounding each act of intergroup aggression may provide insight into what those selective benefits are.

To test this supposition, we collected detailed observations of male participation in naturally occurring intergroup conflicts in a wild population of vervet monkeys. Using this data set, we identified four context-specific types of intergroup aggression exhibited by males: (1) defensive aggression, in response to intergroup aggression by the opposing group; (2) repelling prospecting males, which was the act of chasing away extra-group males that engaged in neutral (e.g. sitting in close proximity) or affiliative (e.g. grooming or playing) interactions with group members; (3) proactive aggression, which was intergroup aggression without a female leader or partner; (4) supporting female instigators, which was when males followed/supported a female leader in initiating intergroup aggression.

In this paper, we first examine male participation during intergroup conflicts as has typically been done in previous studies, treating intergroup aggression as a homogeneous phenomenon. Second, we examine intergroup aggression in each of the four contexts (defensive aggression, repelling prospectors, proactive aggression and supporting female instigators) to determine whether such an approach can provide further insight into the relative importance of the various selective benefits that may drive male participation. If any type of intergroup aggression serves to protect offspring, we predict that it would primarily be exhibited when there are (more) small infants in the group, and by males that were likely to be sires of those infants. If males exhibit intergroup aggression to defend mates, we predict that this type of aggression would be exhibited predominantly by high-ranking males and be more common in the mating season. If intergroup aggression of any type functions as food defence, we predict that it would primarily be exhibited in the summer season, when defensible resources are abundant. Last, if males participate to gain indirect social incentives from females, we would expect this type of aggression to be exhibited primarily during the mating season, and that males that frequently exhibit this type of intergroup aggression should subsequently experience greater mating success.

Methods

Subjects and Study Site

Data were collected on three habituated groups of vervet monkeys at the Mawana Game Reserve (28°00'S, 31°12'E), KwaZulu-Natal, South Africa. Groups consisted of 30–56 individuals and the number of adult males per group ranged from one to seven over the study period. All animals in the three focal groups were individually recognized, as were most of the adults in four neighbouring and frequently encountered groups.

The 22 sampled males were classified as belonging to four different career stages (van Noordwijk and van Schaik 1988) based on their rank and probability of having sired offspring at the time of each intergroup conflict. Matings were recorded on an all-occurrence basis (Altmann 1974), and although low-ranking males did attempt to mate out of sight of the dominant male, the open habitat and frequent terrestrial behaviour of the vervet monkeys meant that matings by both dominant and subordinate males were easily observed by researchers. Thus, the observed matings should be an unbiased sample of the matings that each male actually obtained. For each of the study groups, we calculated the proportion of the observed matings obtained by each male in a given mating season, and classified males having more than 20% of the matings as likely sires. Although we did not use genetic analyses to verify paternity in this study, there is no evidence for paternal kin recognition in this species; therefore, the behavioural proxy we used (i.e. the number of matings males procured, relative to other males in their group) most faithfully represents the information on potential paternity available to the males themselves. Our 20% cutoff was based on the median value of the proportions of matings observed for all males. The mean percentage of matings procured by males below the 20% cutoff was 7%. On average, there were 2.2 males (range 1–3) that were deemed likely sires in each group in a given year, and up to five males with a low probability of having sired offspring (<20% of observed matings). Likely sires were further subdivided into dominant likely sires if they were the alpha male, and subordinate likely sires if they were a subordinate male at the time of the intergroup conflict. Lastly, uninvested males were subordinate males that had not achieved high mating success in their present group.

To determine whether residency time influenced male intergroup aggression, we also classified males as being recent immigrants if they had joined their respective groups within the 60 days preceding the intergroup conflict. This was the maximum length of time that males took to integrate into their group. Similarly, males that would leave their respective groups within the 60 days following the intergroup conflict were deemed future emigrants.

Behavioural Data Collection

Behavioural observations were made between January 2012 and February 2014. Groups were followed an average of 6.5 h per day, five days per week, for a total of >11 000 observation hours. Participation in

intergroup conflicts was recorded on an all-occurrence basis (Altmann 1974). Because concurrent experimental research employed provisioning (van de Waal et al. 2013), we excluded from our analyses all intergroup conflicts occurring on days that provisioning had occurred. We defined the onset of an intergroup encounter when two groups approached within 100 m of each other or initiated vocal interactions over larger distances. At the onset of an intergroup encounter we recorded the time and the location with a handheld GPS unit (Garmin GPSMAP64, Garmin Ltd). Throughout the intergroup conflict, we recorded all participation events for each individual in the focal group and also noted the participation of the opposing group's members whenever possible. Intergroup encounters were deemed intergroup conflicts when one or more individuals from either group exhibited aggression to the opposing group. For each aggressive participation event, we recorded the identity of active individuals, the identity of the individual that instigated/led the event, behaviour(s) exhibited, identity of the target individuals (or their sex and age class when their identity was unknown), and whether the aggressive behaviour was proactive (instigated by the focal group) or reactive (in response to aggression by the opposing group). Aggressive behaviours could be directed towards the opposing group as a whole (e.g. running at the group or making aggressive displays and/or vocalizations) or target specific individuals (e.g. chasing or biting).

GPS Data and Home Range Estimation

Previous studies have shown that individuals are more likely to exhibit aggression closer to the centre of their home range or in intensely used areas, and as a result groups are more likely to win conflicts in these locations (Crofoot and Gilby 2012; Markham et al. 2012). To account for this potentially confounding effect of location, we determined both the distance from each intergroup conflict location to the home range centre and the long-term intensity of use. We deployed a GPS collar (e-obs Type 1C light, e-obs GmbH) on one adult female in each group, and programmed it to obtain GPS-fixes every 30 min, from 0500 to 1900 hours, between March 2013 and February 2014. Over this period, utilization distributions were estimated for each group using the Brownian bridge movement model (Horne et al. 2007) as implemented by (Buchin et al. 2012) in R (version 3.0.2, R Core Team 2014). Fixes from the beginning, and end, of the day that were within 50 m of the start, and finish, locations, were censored to restrict our calculations to the diurnal activity period of the animals. After estimating the utilization distribution, we used the 99% isopleth to delineate home range boundaries, and from this calculated the home range centroid. For each intergroup conflict location, we determined the local intensity of use from the estimated utilization distribution, and the distance to the home range centroid. Intensity of use values were reciprocal-log transformed in order to stabilize our statistical models and ensure convergence of maximum-likelihood parameter estimates. Although we did not have GPS location data across the entire study period, the observed range use of all three focal groups was stable between years. Thus, areas

of higher intensity of use in the period with active GPS loggers suitably represented the longer-term value of an area for the purpose of this study.

Habitat Productivity

The summer season was indexed using monthly average normalized difference vegetation index (NDVI) values from the MODIS MCD43A4 data set (version 5, processed by NASA's LP DAAC (NASA Land Processes Distributed Active Archive Center (LP DAAC) 2014) and redistributed by WAMIS at http://wamis.meraka.org/za/). The NDVI is a well-established proxy of the amount and vigour of green vegetation, and strongly correlates with field measurements of food availability and shelter in vervet monkeys (Willems et al. 2009). Over the study period, monthly average NDVI values ranged from 0.25 to 0.67 with larger values occurring during the summer months, and indicating denser and more photosynthetically active vegetation.

Statistical Analyses

We included male career stage and residency status as independent factors in our analyses of intergroup aggression. We also included four seasonal factors (the onset of the birth season, the birth season, the summer season and mating season), the intensity of use of the intergroup conflict location, distance to the home range centre and the asymmetry in group size as independent factors. The first infants were typically born in September or October. We included the first month of the birth season (30 days following the first birth in the group: yes or no) in our analyses to test whether males were more aggressive when they first became likely sires. We indexed the birth season using the number of small infants in the group (i.e. number of individuals less than three months old). The summer season was indexed using monthly NDVI values to account for seasonal changes in resource (food and shelter) abundance (Willems et al. 2009); above-average NDVI values typically occurring between December and May. We classified the mating season as months in which the average mating rate was greater than two matings per 100 observation hours (April to August 2012; April to July 2013). Last, because previous studies have shown that individuals may modulate their participation in intergroup conflicts according to the relative fighting ability of their group, being active primarily when their group is outnumbered and their participation is most needed (Heinsohn and Packer 1995; Kitchen 2006), we also considered the effect that asymmetry in group size had on male participation. Relative group size was defined as the relative number of adults and subadults in the focal group minus the number in the opposing group. We included adults and subadults as these were the two age classes that typically participated aggressively during intergroup conflicts.

All statistical analyses were conducted in R (version 3.0.3, R Core Team 2014) using the lme4 package (version 1.1-4, Bates et al. 2015) and nlme packages (version 3.1-113, Pinheiro and Bates 2014). In our first analysis, we built a generalized linear mixed model (GLMM) to test the relative importance of the various independent factors (e.g. male career stage, residency, season, location and relative group size) in explaining whether or not males behaved aggressively during intergroup conflicts. In this first analysis, all aggressive acts were treated as a homogeneous phenomenon as we did not take into account the context in which they occurred. In our second set of analyses we used four separate GLMMs to investigate which factors influenced whether males (1) exhibited defensive aggression, (2) repelled prospecting males, (3) exhibited proactive aggression or (4) supported female instigators during intergroup conflicts.

In all GLMMs the response variable was binary, and we therefore set a binomial error structure and logit link function in our models. We included male identity nested within group as random effects in all models to account for repeated sampling of individuals (Zuur et al. 2009). When we tested the effect of male career stage, uninvested males were always coded as the reference category. When both dominant and subordinate likely sires showed a similar pattern of behaviour, but one showed a significant effect and the other only a trend, we pooled all sires, regardless of their rank, and reran the model to determine the overall effect of being a likely father (in each case, both models are presented in the Chapter 2 Appendix). Doing so had very little effect on parameter estimates.

We tested the significance of five interaction terms (male career stage * month following first birth, male career stage * number of small infants, male career stage * monthly average NDVI, male career stage * mating season, and number of small infants * relative group size) in each GLMM with likelihood ratio tests (χ^2 test statistic), comparing the model with only main effects included to the model with each interaction included (Bolker et al. 2009; Zuur et al. 2009). Interactions that did not improve model fit at the significance level of $\alpha = 0.1$ were not retained in the final model. In all analyses, α was set at 0.05, but we briefly discuss nonsignificant trends ($p < 0.10$) when they are biologically interesting.

To test whether any of the four types of intergroup aggression were related to male mating success, we used linear mixed-effects models (LMMs). We tested whether the proportion of intergroup conflicts in which males exhibited each aggression type (between January and the end of the mating season) correlated with their subsequent mating success that year. We excluded males that immigrated at the end of the mating season (were not present for at least three intergroup conflicts) from these analyses. The response variable, individual daily mating rate, was arcsine-square-root transformed prior to analysis, and we included individual male identity nested within group as a random effect (Zuur et al. 2009).

We based our inferences on full models (plus important interaction effects) rather than using a stepwise procedure to avoid false positives and biased effect size estimates (Forstmeier and Schielzeth 2011). Following statistical convention we did not interpret main effects if the predictor variable featured in a significant interaction effect. The overall significance of each GLMM was assessed by comparing the final model to the null model (model including intercept and random effects only) using a likelihood ratio test, while the total variance explained ($R^2_{GLMM(c)}$) was estimated following the method described by Nakagawa and Schielzeth (Nakagawa and Schielzeth 2013). For LMM models, we present the marginal rather than conditional R^2_{LMM} because we were only interested in the variance explained by the fixed effects.

Ethical Note

All data collection protocols were approved by local and national authorities, as well as the Ezemvelo KZN Wildlife Ethics Board in South Africa. In the course of this study period we trapped nine adult females in the three main study groups in order to outfit each with a GPS collar. We modified the trapping method used by Grobler and Turner (Grobler and Turner 2010) so that researchers could use a rope to trigger the trap and target the desired individual (i.e. an adult female). Once captured, females were tranquillized with ketamine, weighed, and a GPS collar fitted before they were released. After being released in a shady and covered location, females were observed until they had recovered and returned to their group. The weight of GPS collars was 120 g, which is equivalent to approximately 3% of the body weight of the smallest adult female that we collared. GPS collars were active for four to five months before the battery failed; thus, we deployed GPS collars onto three females in each of the three groups to obtain one year of continuous movement data.

Results

In total, we observed more than 400 intergroup encounters, half of which escalated into an intergroup conflict. We restricted our analyses to a subset of 126 intergroup conflicts in which all independent factors were known. On average, an individual male was only aggressive in a quarter of the intergroup conflicts that his group experienced, but participation was highly variable among the 22 males (mean proportion of encounters ± SD: 0.25 ± 0.20; Figure 2.2). The most frequently observed types of aggression were defensive aggression (0.08 ± 0.12), repelling prospecting males (0.06 ± 0.08) and supporting instigator females (0.10 ± 0.10). Conversely, males rarely instigated proactive aggression without a female partner (0.03 ± 0.05).

Treating Acts of Intergroup Aggression as Homogeneous

In our first analysis, in which we did not differentiate between acts of intergroup aggression within intergroup conflicts, we found that male career stage was an important predictor of male intergroup aggression.

Dominant likely sires were more likely to behave aggressively during intergroup conflicts than uninvested males (subordinate males that were unlikely to have sired offspring), particularly when there were more small infants in the group (Figure 2.3a; Table A2.1). Subordinate likely sires showed a similar pattern of participation, but the interaction term just failed to reach statistical significance (Figure 2.3a; Table A2.1). However, when we pooled all likely sires, regardless of their rank, an overall positive interaction between the number of small infants in the group and being a likely sire was apparent (Table A2.2). Males were more likely to be aggressive in the first month of the birth season than during the rest of the year (Table A2.2), and males tended to exhibit intergroup aggression more if there were small infants in the group and their group was at a numerical disadvantage (Figure 2.3b; Table A2.2). Alternatively, when there were small infants in the group and their group was at a numerical advantage, males were the least active in intergroup conflicts. Thus, males, and likely sires in particular, appeared to be sensitive to the risk that intergroup conflicts posed to probable offspring. Males that had recently immigrated tended to participate in intergroup conflicts less frequently than other males (Table A2.2). We detected no effect of seasonal resource abundance, mating season, the annual intensity of use of the conflict location or the distance to the home range centre on the probability that males were aggressive during intergroup conflicts (Table A2.2).

Context 1: Defensive Intergroup Aggression

In our second set of analyses, we classified acts of intergroup aggression into four categories according to the context in which the aggression was exhibited. We found that likely sires were more likely to exhibit defensive intergroup aggression, although dominant and subordinate likely sires did not show the same strength of response. Subordinate likely sires were more likely to reactively defend their group members than uninvested males, while dominant likely sires showed only a tendency to do the same (Table A2.3). However, when we pooled all likely sires, regardless of their rank, we found that a high likelihood of paternity was associated with higher frequencies of defensive aggression (Table A2.4). In contrast, dominant males without a high likelihood of paternity showed no greater tendency to exhibit defensive aggression than did uninvested males (Table A2.4). Males used defensive aggression independent of season, location and relative group size (Table A2.4).

Context 2: Repelling Prospecting Males

Dominant likely sires showed a stronger tendency to repel prospecting males than subordinate likely sires (Table A2.5) but overall, males that were likely sires were more likely to exhibit this type of intergroup aggression than uninvested males (Table A2.6). There was a weak tendency for males to exhibit intergroup aggression in this context during the summer season, when high-quality food resources were abundance (Table A2.6). This was the time of year that intergroup conflicts were frequent and of a long duration, and

therefore when males had the most opportunities to prospect. Males repelled prospecting males independent of the immigration status, season, location and relative group size (Table A2.6).

Context 3: Proactive Intergroup Aggression

Proactive aggression was also more likely to be exhibited by likely sires than uninvested males, regardless of whether they were dominant or subordinate (Table A2.7). In contrast, dominant males without a high likelihood of paternity showed no greater tendency to exhibit proactive aggression than did uninvested males (Table A2.7). Intergroup aggression in this context was rare (Figure 2.2), but we never observed recent immigrants exhibiting proactive aggression. We found no significant season or location effects in this context, and relative group size was also unimportant (Table A2.7).

Context 4: Supporting Female Instigators

In the context of supporting female instigators, males showed different patterns of intergroup aggression than they did in the other three contexts. Importantly, males were significantly more likely to support female instigators during the mating season than other times of year (Table A2.8; Table A2.9). We also found a significant interaction between male career stage and the summer season, indicating that dominant males tended to start supporting female instigators two to three months prior to the onset of the mating season, as this is the time when NDVI values tended to be greater than 0.5 (Figure 2.4; Table A2.9). This tendency, however, was weaker for dominant likely sires than dominant unlikely sires (Figure 2.4; Table A2.8). We detected no significant effect of the number of small infants in the group, location or relative group size (Table A2.9). There was a weak tendency for males to exhibit this type of aggression during the first month of the birth season (Table A2.9).

Male Intergroup Aggression and Subsequent Mating Success

We found that the propensity to exhibit intergroup aggression in all four contexts was at least weakly associated with subsequent mating success (Figure 2.5). However, only intergroup aggression in the context of supporting female instigators showed a strong correlation; the frequency that individual males exhibited this type of intergroup aggression explained approximately a third of the variability in male mating success (LMM: $R^2_{LMM(m)} = 0.28$, $t = 3.28$, $p = 0.008$; Figure 2.5d). Furthermore, intergroup aggression to support female instigators explained almost twice as much variation in the subsequent mating success of individual males than did exhibiting defensive aggression ($R^2_{LMM(m)} = 0.15$, $t = 2.23$, $p = 0.050$**;** Figure 2.5a), repelling prospectors ($R^2_{LMM(m)} = 0.15$, $t = 2.26$, $p = 0.047$; Figure 2.5b) or proactive aggression ($R^2_{LMM(m)} = 0.14$, $t = 2.19$, $p = 0.053$;

Figure 2.5c). We observed relatively low mating skew such that on average there were 2.2 males per group that obtained >20% of the matings in a given year. Thus, the observed relationship between supporting female instigators and individual mating success was not simply a dominance effect, as there were usually one or two subordinate males that were relatively successful in obtaining mating opportunities.

Discussion

The aim of this study was to determine the relative importance of various individual benefits and social incentives in modulating male aggression during intergroup conflicts. By considering the social and ecological context surrounding each act of intergroup aggression, we found evidence for two selective benefits of male participation in intergroup conflicts. Our findings suggest that likely sires employed an offspring defence strategy, and that males also support of female instigators during and just prior to the onset of the mating season to gain status as a good cooperative partner, and subsequently enhance their mating success. We found little evidence that males fight in intergroup conflicts to directly defend food or mates, and, unlike other studies (e.g., Crofoot et al. 2008; Markham et al. 2012), we detected no effect of location.

Evidence for Offspring Defence

When we examined intergroup aggression as a homogeneous behavioural phenomenon, we found that likely sires were those most likely to participate in intergroup conflicts, indicating that offspring protection may be an important selective benefit of male intergroup aggression in vervet monkeys. Males were more likely to exhibit intergroup aggression when there were (more) small infants present, and when being at a numerical disadvantage could increase the risk of injury or death for group members (Mosser and Packer 2009; Sillero-Zubiri and Macdonald 1998). In many of the intergroup conflicts that we observed, the group that was at a numerical disadvantage made little attempt to defend a given location, and fled as the larger group approached. On numerous occasions, we observed that infants were at risk of being left behind, presumably when they had strayed too far from their mothers and could not be collected quickly as the group fled. When left behind, infants were attacked by members of the opposing group; as has also been reported in other studies (Cheney and Seyfarth 1987), these attacks could result in death. To mitigate this risk, males from numerically inferior groups often ran to meet the opposing group and exhibited defensive aggression, seemingly to ensure that their fleeing group members escaped safely. Conversely, the reduced need for males in larger groups to respond defensively may explain why we found that males in numerically superior groups were less likely to participate aggressively during intergroup conflicts when there were small infants in the group. Together, anecdotal and empirical evidence supports the hypothesis that escalated intergroup conflicts pose a risk to potential offspring, such that likely sires may gain fitness benefits by acting as protective parents.

Males often chase away extra-group males that are attempting to affiliate with group members during intergroup encounters, and this tendency has been cited as evidence for mate defence in vervet monkeys (Cheney 1981). Because dominant males typically experienced the greatest mating success, we expected that they, rather than likely sires, would exhibit aggression in this context if prospecting males were perceived primarily as mating competitors. However, we found it was likely sires that were most likely to repel prospecting males, suggesting that the latter are not perceived as future competition, but rather as a threat to potential offspring. Anecdotally, prospecting males were often tolerated in close proximity for long periods, and curious juveniles were those most likely to approach closely and interact with them. It was often after a conflict between juveniles and prospecting males that the latter were chased away.

Previous evidence of offspring defence has primarily been found in species with high paternity certainty and frequent infanticide (e.g., Kitchen 2004; Wich et al. 2004). To our knowledge, our results are the first to indicate that male intergroup aggression can function as paternal care in a species with multi-male groups and low paternity certainty. In the absence of kin recognition, males may evaluate their probability of paternity based on their past mating success (Moscovice et al. 2010), and when intergroup conflicts pose a threat to offspring survival, males may gain fitness benefits by defending likely offspring, even in the face of paternity uncertainty.

Evidence for Mate Defence

The only context in which we saw a significant mating season effect was in supporting female instigators. While this finding may superficially seem to support a mate defence strategy, it is unlikely given other evidence. If male aggression during the mating season provided an individual benefit, we would expect that males would be equally as likely to exhibit this type of aggression without a female partner; however, proactive intergroup aggression was extremely rare, and did not show the same seasonal pattern. Thus, it seems likely that an alternative mechanism can better explain this mating season effect.

Evidence for Food Defence

Dominant males were more likely to support female instigators during the summer months, when high-quality food resources were abundant. Again, given that proactive intergroup aggression was rare, and did not show the same seasonal pattern, it is unlikely that dominant males exhibit this type of aggression to defend food directly, and that an alternative explanation is required for this interaction term.

Evidence for Social Incentives

We found a significant effect of mating season on the tendency of males to support female instigators. Furthermore, dominant males tended to start exhibiting this type of intergroup aggression in the summer months, before the onset of the mating season. This period (i.e. approximately December to February) is typically characterized by the presence of high-quality fruits and high NDVI values, and is when females were most active in intergroup conflicts. Given that males that displayed this type of intergroup aggression were following female leaders, and therefore cooperating with females to defend valuable resources, there is a strong possibility that this type of intergroup aggression is motivated by social incentives rather than individual benefits. Indirect social incentives are a feasible mechanism for promoting male participation in intergroup conflicts in this species because of the extent to which females can choose their mating partners. Females were often observed to refuse matings with both dominant and subordinate males, regardless of differences in body size. Some males were frequently denied copulations, while others were almost never refused, indicating that females have preferences among male group members. Furthermore, male mating success was strongly related to the proportion of intergroup conflicts in which they had supported female instigators. Together, these findings suggest that males probably support females in fighting for valuable resources to either advertise their quality or to build status with female group members, the benefits of which can be reaped during the subsequent mating season. In species where females are able to use social incentives to exert leverage over males, cooperation may be sexually selected for through female preferences for cooperative males, and males would more accurately be characterized as 'Reluctant Recruits' than 'Hired Guns'.

Although other authors have previously proposed that males may use participation in intergroup conflicts in order to impress females and subsequently gain access to mates (Fashing 2001; Steenbeek 1999), we present the first evidence, outside of humans, that intergroup aggression can be associated with increased mating success (Chagnon 1988; Glowacki and Wrangham 2015; Glowacki and Wrangham 2013). To further delineate which mechanism best explains the patterns of behaviour observed in vervet monkeys (i.e. social prestige versus direct and/or indirect reciprocity mechanisms), future studies would have to determine whether male intergroup aggression is an honest signal of male quality and the extent to which group members observe and use information on male participation in making future mating decisions (Bergmüller et al. 2007).

In this study, we demonstrated that apparent food or mate defence is not easily interpreted in species with female choice. Similar caution should be taken in interpreting findings in species in which females can disperse to access preferred males, or in which group members form coalitions. In such cases, seasonal variability in participation could indicate either that intergroup aggression is driven by individual benefits, or that individuals fight in intergroup conflicts to obtain social incentives. When working on species in which social

incentives may be used to influence intergroup aggression, it is important to consider both the ecological and the social context in which individuals participate. Social context could be 'with whom individuals cooperate' during intergroup conflicts, as was examined in this study, or 'whose presence' influences individual participation (e.g., Meunier et al. 2012).

Elucidating Individual Variability by Considering Context

Despite the important role that individual variability plays in overcoming collective action problems in theoretical models (Gavrilets and Fortunato 2014), we are unaware of any study on intergroup conflict that illustrates that multiple selective benefits promote male intergroup aggression. In our first analysis, we did not differentiate between acts of aggression within intergroup conflicts; thus, all acts of aggression were treated as a homogeneous phenomenon. With this approach, we only detected an offspring defence strategy, probably because it was the most frequently expressed mechanism. It was only when we partitioned acts of intergroup aggression according to context that we elucidated an alternative strategy, namely acting as a 'Reluctant Recruit' in order to obtain social incentives.

If intergroup conflicts pose a risk to infants (as was observed in this study, as well as Cheney 1987), escalating intergroup conflicts could have fitness consequences for males that are likely to have sired offspring. Indeed, we saw that likely sires were more likely to exhibit reactive aggression, becoming involved in the intergroup conflict only when the opposing group was being aggressive rather than instigating intergroup aggression themselves. Alternatively, failing to support females in instigating intergroup aggression could have negative consequences, impacting their mating success in the following mating season. Thus, likely sires may face a trade-off between their future mating success and the safety of their current probable offspring. Depending on their probability of paternity, the season and their ability to fight in intergroup conflicts, individual males probably experience a unique set of costs and benefits from participating or defecting. The observed 'group behaviour' in any given intergroup conflict emerges from the sum total of the decisions made by each individual group member. As a result, the public good of home range defence can be produced by different individuals, in different seasons or even at different times within a single intergroup conflict. Our findings highlight that investigations of group-level cooperation must quantify the various selective benefits that influence the decisions of all group members, and not only the selective benefit that is most frequently expressed. Collective action problems can pose a significant challenge to group-level cooperation (Nunn and Lewis 2001; Willems et al. 2013), and our study has advanced our understanding of the mechanisms by which collective action problems may be averted. However, a comprehensive examination of group-level cooperation requires an understanding of not just the selective benefits driving male participation, but also female intergroup aggression, as well as the factors influencing the effectiveness of cooperation between

group members with diverging interests. Such investigations will enrich our understanding of the mechanisms by which intergroup conflict exerts selective pressure on the evolution of cooperation in social species, including our own (Bowles 2009; van Schaik 1983; Wrangham 1980).

Chapter 2 Figures

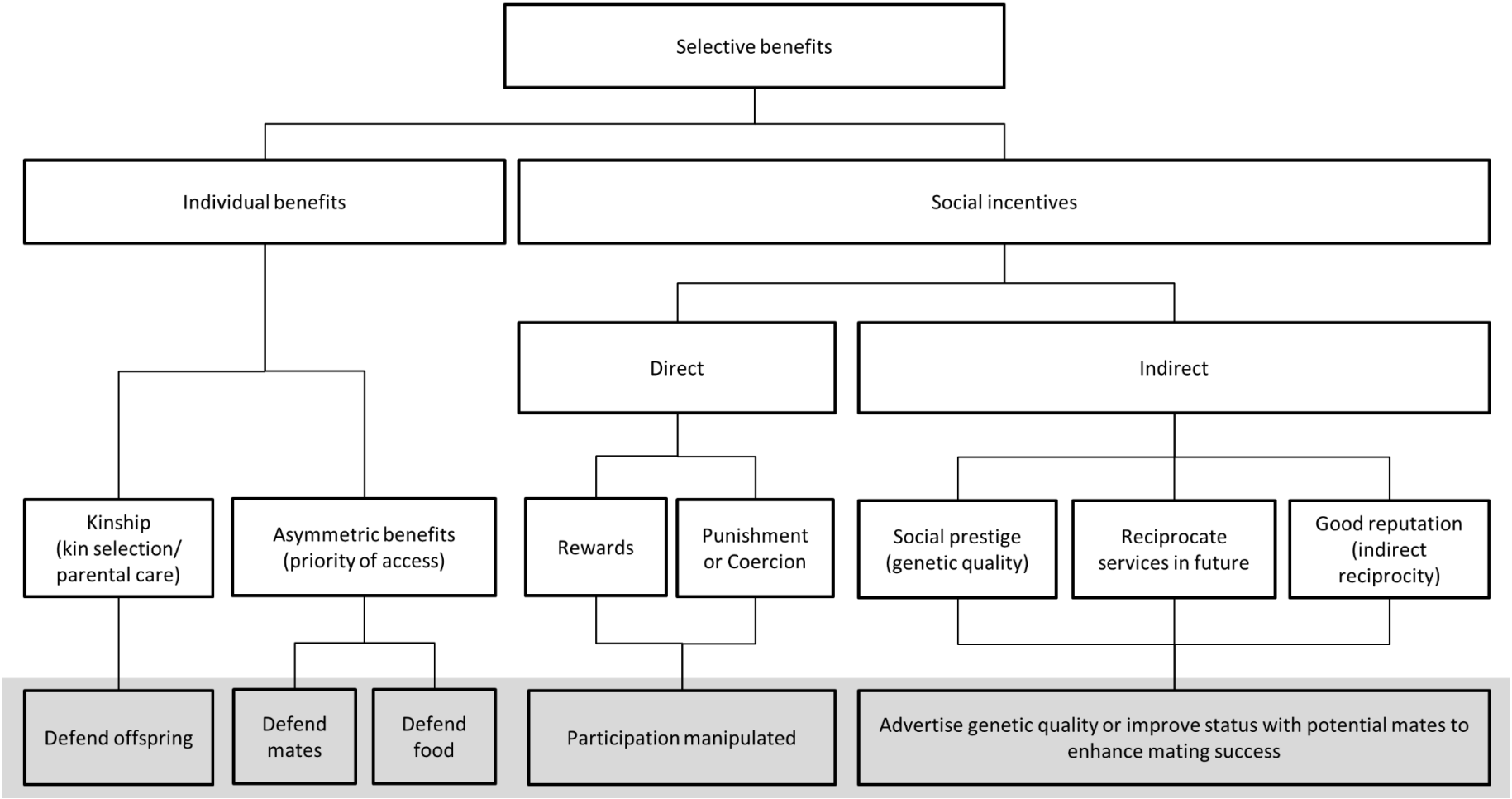

Figure 2.1 Potential selective benefits of cooperation in a social group (white background) (adapted from Bergmüller et al. 2007; Bshary and Bergmüller 2008; Fashing 2001; Nunn and Lewis 2001) and associated reasons for male vervet monkeys' participation in intergroup conflicts (grey background).

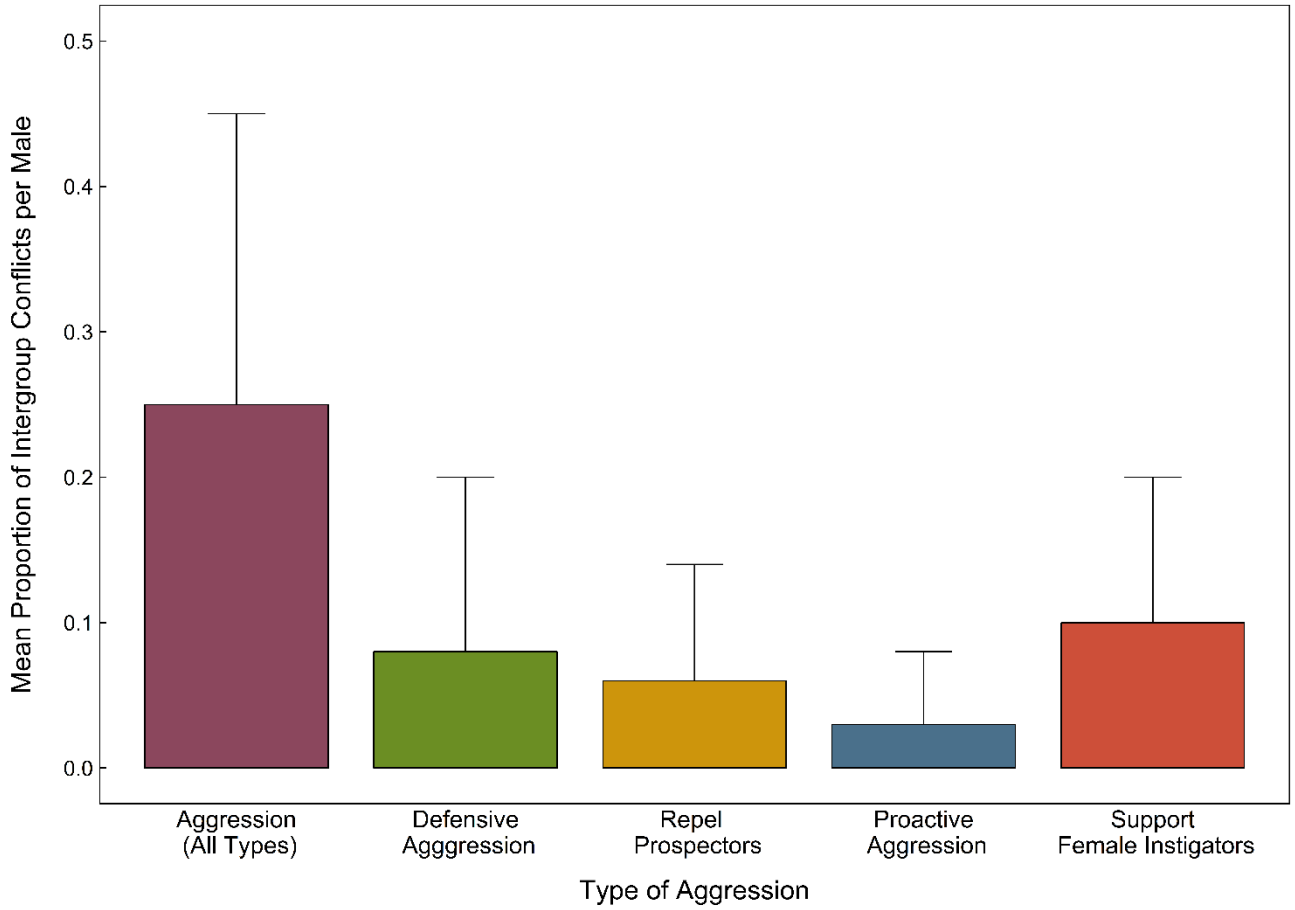

Figure 2.2 Mean proportion of intergroup conflicts in which males participated aggressively and exhibited each type of context-specific, intergroup aggression. Error bars depict SD.

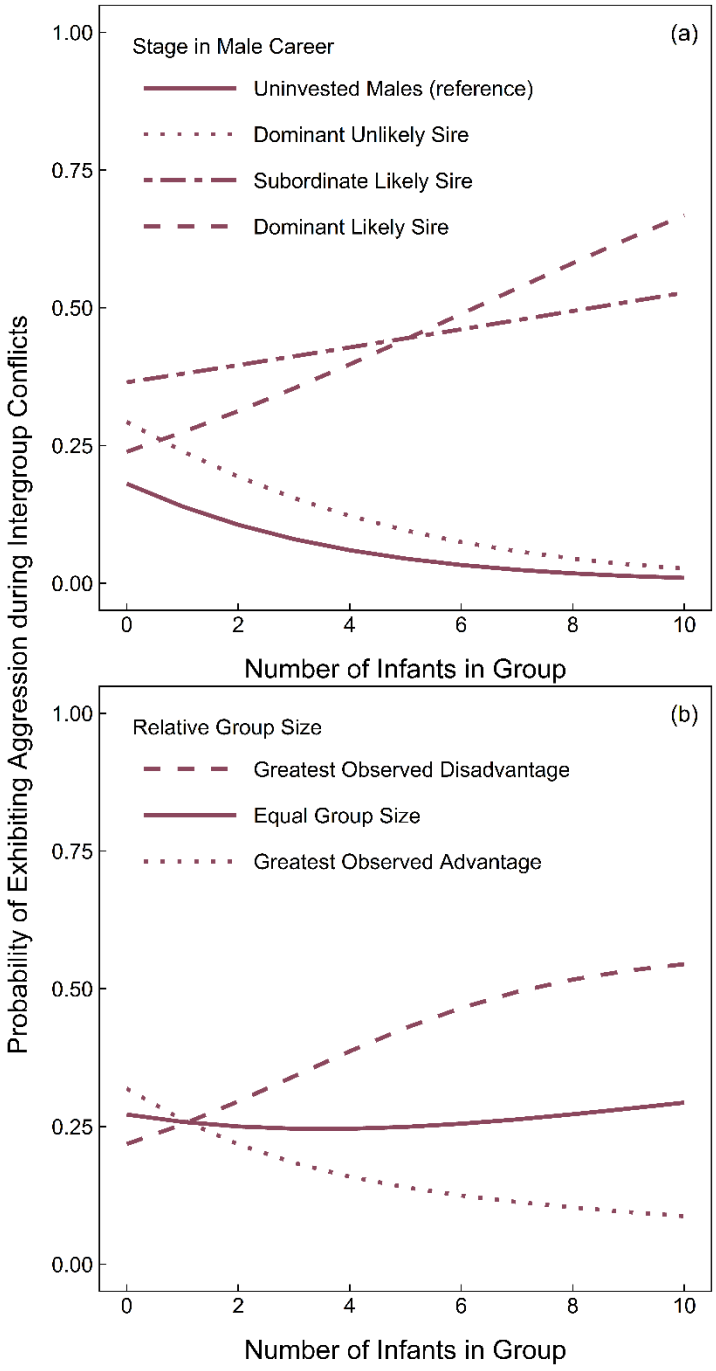

Figure 2.3 Probability of a male participating aggressively during intergroup conflicts as a function of (a) the interaction between male career stage and number of small infants in the group and (b) the interaction between relative group size and the number of small infants in the group. Prediction lines were obtained by plotting GLMM predictions (Table A2.1), setting all additional predictor variables to their mean values.

In (b), we averaged predicted probabilities across the four categories of male career stage to illustrate the expected probability of aggression for an average male in our population.

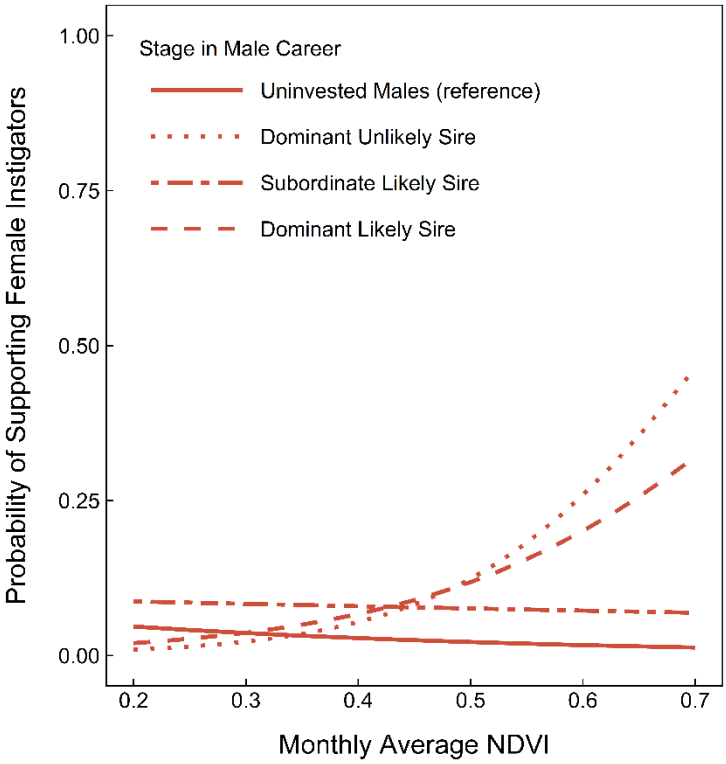

Figure 2.4 Probability that males supported female instigators during intergroup conflicts, as a function of the interaction between male career stage and the monthly average NDVI values, a proxy of seasonal resource abundance. Prediction lines were obtained by plotting GLMM predictions (Table A2.8), setting all additional predictor variables to their mean values.

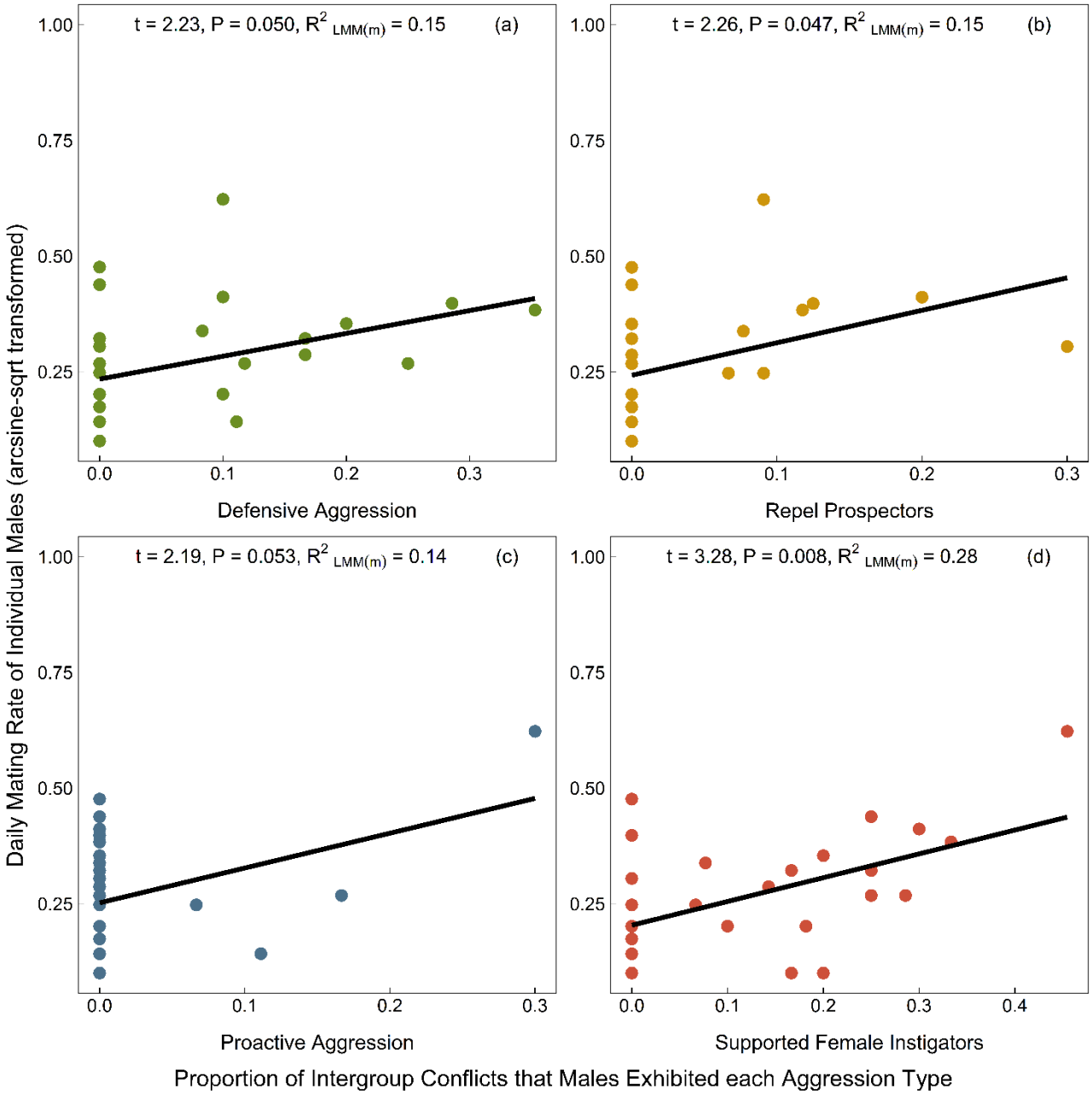

Figure 2.5 Linear mixed-effects models of the relationship between the proportion of intergroup encounters that males (a) exhibited defensive aggression, (b) repelled prospectors, (c) exhibited proactive aggression and (d) supported female instigators and their subsequent mating success. Each male's daily mating rates were arcsine-square-root transformed prior to analyses.

Chapter 2 Appendix

Table A2.1 Factors affecting the probability that males were aggressive (aggression as a homogeneous phenomenon) during intergroup conflicts, after nonsignificant interaction terms were removed from the model.

Fixed Effects	***b* Estimate**	**SE**	***z***	***p***
(Intercept)	-1.23	1.36	-	-
Male career stage				
Uninvested males (reference category)	-	-	-	-
Dominant unlikely sire	0.65	0.50	-	-
Subordinate likely sire	0.95	0.40	-	-
Dominant likely sire	0.35	0.45	-	-
Residency				
Immigrant	**-0.66**	**0.35**	**-1.86**	**0.064**
Emigrant	0.09	0.36	0.25	0.801
Seasonal factors				
Month following first birth	**1.39**	**0.57**	**2.43**	**0.015**
Number of small infants	-0.32	0.17	-	-
Seasonal habitat productivity	1.65	1.14	1.44	0.150
Mating season	0.45	0.33	1.34	0.180
Intensity of use	-0.08	0.12	-0.65	0.514
Distance to home range centre	-0.03	0.05	-0.66	0.510
Relative group size	0.03	0.05	-	-
Interactions				
*Number of small infants * Relative group size*	*-0.03*	*0.02*	*-1.73*	*0.084*
Number of small infants * Dominant unlikely sire	0.04	0.38	0.10	0.920
*Number of small infants * Subordinate likely sire*	*0.38*	*0.21*	*1.76*	*0.079*
Number of small infants * Dominant likely sire	**0.50**	**0.20**	**2.43**	**0.015**

The final model was significantly different from the null model containing only an intercept term and individual nested in group as random effects (likelihood ratio test: $n = 351$, $\chi^2 = 80.43$, $p < 0.001$, $R^2_{GLMM(c)} = 0.23$). Male career stage was always compared to uninvested males as a reference category. The removed nonsignificant interactions were those between male career stage and whether it was the month following the first birth of the season or not ($n = 351$, $\chi^2 = 0.91$, $p = 0.635$), male career stage and seasonal habitat productivity ($N = 351$, $\chi^2 = 2.57$, $p = 0.463$) and male career stage and mating season ($n = 351$, $\chi^2 = 1.24$, $p = 0.742$). Significant predictors are presented in bold and trends are italicized.

Table A2.2 Factors affecting the probability that males were aggressive during intergroup conflicts (aggression as a homogeneous phenomenon), with all likely sires pooled, regardless of their rank.

Fixed Effects	***b* Estimate**	**SE**	***z***	***p***
(Intercept)	-1.44	1.40	-	-
Male career stage				
Uninvested males (reference category)	-	-	-	-
Dominant unlikely sire	0.59	0.53	-	-
All likely sires (pooled)	0.65	0.38	-	-
Residency				
Immigrant	*-0.70*	*0.36*	*-1.92*	*0.051*
Emigrant	0.10	0.37	0.27	0.787
Seasonal factors				
Month Following first birth	**1.38**	**0.58**	**2.37**	**0.018**
Number of small infants	-0.32	0.17	-	-
Seasonal habitat productivity	1.70	1.17	1.46	0.146
Mating season	0.45	0.34	1.34	0.180
Intensity of use	-0.06	0.12	-0.49	0.622
Distance to home range centre	-0.03	0.05	-0.60	0.547
Relative group size	0.05	0.05	-	-
Interactions				
*Number of small infants * Relative group size*	*-0.03*	*0.02*	*-1.91*	*0.056*
Number of small infants * Dominant unlikely sire	0.04	0.39	0.12	0.908
Number of small infants * All likely sires	**0.43**	**0.19**	**2.26**	**0.024**

The final model was significantly different from the null model containing only an intercept term and individual nested in group as random effects (likelihood ratio test: $n = 351$, $\chi^2 = 79.56$, $p < 0.001$, $R^2_{GLMM(c)} = 0.24$). Male career stage was always compared to uninvested males as a reference category. Significant predictors are presented in bold and trends are italicized.

Table A2.3 Factors affecting the probability that males exhibited defensive (reactive) aggression to protect group members during intergroup conflicts**,** after nonsignificant interaction terms were removed from the model.

Fixed Effects	***b* Estimate**	**SE**	***z***	***p***
(Intercept)	-5.50	2.26	-	-
Male career stage				
Uninvested males (reference category)	-	-	-	-
Dominant unlikely sire	-0.24	0.82	-0.29	0.770
Subordinate likely sire	**1.14**	**0.55**	**2.07**	**0.038**
Dominant likely sire	*1.11*	*0.60*	*1.83*	*0.067*
Residency				
Immigrant	-0.00	0.56	-0.00	0.998
Emigrant	-0.02	0.56	-0.03	0.978
Seasonal factors				
Month following first birth	0.32	0.78	0.41	0.685
Number of small infants	0.08	0.09	0.89	0.375
Seasonal habitat productivity	1.66	1.89	0.88	0.380
Mating season	0.27	0.53	0.52	0.607
Intensity of use	-0.12	0.22	-0.57	0.570
Distance to home range centre	0.37	0.26	1.43	0.153
Relative group size	-0.02	0.08	-0.24	0.809

The final model was significantly different from the null model containing only group and individual as random effects (likelihood ratio test: n = 345, χ^2 = 23.15, p = 0.026, $R^2_{GLMM(c)}$ = 0.53). Male career stage was always compared to uninvested males as a reference category. The removed nonsignificant interactions were those between male career stage and seasonal habitat productivity (n = 345, χ^2 = 1.91, p = 0.591), male career stage and mating season (n = 345, χ^2 = 4.66, p = 0.198) and relative group size and the number of small infants (n = 345, χ^2 = 1.32, p = 0.251). The model failed to converge when the interactions between male career stage and the number of small infants and male career stage and whether it was the month following the first birth of the season or not were included; therefore, we could not evaluate the significance of these interactions. Significant predictors are presented in bold and trends are italicized.

Table A2.4 Factors affecting the probability that males exhibited defensive (reactive) aggression to protect group members during intergroup conflicts, with all likely sires pooled.

Fixed Effects	***b* Estimate**	**SE**	***z***	***p***
(Intercept)	-5.52	2.23	-	-
Male career stage				
Uninvested males (reference category)	-	-	-	-
Dominant unlikely sire	-0.24	0.82	-0.30	0.767
All likely sires (pooled)	**1.13**	**0.48**	**2.36**	**0.018**
Residency				
Immigrant	-0.00	0.56	-0.00	0.997
Emigrant	0.01	0.56	0.03	0.979
Seasonal factors				
Month following first birth	0.32	0.77	0.41	0.679
Number of small infants	0.08	0.09	0.89	0.375
Seasonal habitat productivity	1.68	1.87	0.90	0.371
Mating season	0.27	0.53	0.52	0.604
Intensity of use	-0.13	0.21	-0.58	0.559
Distance to home range centre	0.37	0.25	1.51	0.130
Relative group size	-0.02	0.07	-0.24	0.810

The final model was significantly different from the null model containing only group and individual as random effects (likelihood ratio test: n = 345, χ^2 = 23.15, p = 0.017, $R^2_{GLMM(c)}$ = 0.53). Male career stage was always compared to uninvested males as a reference category. Significant predictors are presented in bold and trends are italicized.

Table A2.5 Factors affecting the probability that males repelled prospecting extra-group males during intergroup conflicts**,** after nonsignificant interaction terms were removed from the model.

Fixed Effects	***b* Estimate**	**SE**	***z***	***p***
(Intercept)	-3.81	2.41	-	-
Male career stage				
Uninvested males (reference category)	-	-	-	-
Dominant unlikely sire	0.47	0.88	0.54	0.590
Subordinate likely sire	*1.15*	*0.66*	*1.75*	*0.080*
Dominant likely sire	**1.71**	**0.65**	**2.64**	**0.008**
Residency				
Immigrant	-1.29	0.83	-1.57	0.118
Emigrant	0.48	0.62	0.78	0.438
Seasonal factors				
Month following first birth	-0.56	1.17	-0.48	0.632
Number of small infants	-0.16	0.13	-1.23	0.220
Seasonal habitat productivity	*3.49*	*2.04*	*1.71*	*0.088*
Mating season	-0.16	0.64	-0.24	0.809
Intensity of use	-0.05	0.21	-0.24	0.813
Distance to home range centre	-0.07	0.09	-0.74	0.459
Relative group size	0.04	0.08	0.49	0.625

The final model was significantly different from the null model containing only group and individual as random effects (likelihood ratio test: n = 351, χ^2 = 34.64, $p < 0.001$, $R^2_{GLMM(c)}$ = 0.26). Male career stage was always compared to uninvested males as a reference category. The removed nonsignificant interactions were those between male career stage and the number of small infants (n = 351, χ^2 = 1.21, p = 0.752), male career stage and seasonal habitat productivity (n = 351, χ^2 = 1.32, p = 0.725), male career stage and mating season (n = 351, χ^2_3 = 1.70, p = 0.637) and relative group size and the number of small infants (n = 351, χ^2 = 0.02, p = 0.877). The model failed to converge when the interaction between male career stage and whether it was the month following the first birth of the season or not was included; therefore, we could not evaluate the significance of this term. Significant predictors are presented in bold and trends are italicized.

Table A2.6 Factors affecting the probability that males repelled prospecting extra-group males during intergroup conflicts, with all likely sires pooled.

Fixed Effects	***b* Estimate**	**SE**	***z***	***p***
(Intercept)	-3.78	2.41	-	-
Male career stage				
Uninvested males (reference category)	-	-	-	-
Dominant unlikely sire	0.50	0.88	0.57	0.566
All likely sires (pooled)	**1.42**	**0.56**	**2.51**	**0.012**
Residency				
Immigrant	-1.28	0.83	-1.56	0.120
Emigrant	0.42	0.62	0.68	0.494
Seasonal factors				
Month following first birth	-0.50	1.16	-0.43	0.666
Number of small infants	-0.15	0.13	-1.19	0.236
Seasonal habitat productivity	*3.46*	*2.02*	*1.71*	*0.087*
Mating season	-0.17	0.64	-0.27	0.786
Intensity of use	-0.05	0.21	-0.23	0.819
Distance to home range centre	-0.07	0.09	-0.81	0.416
Relative group size	0.02	0.07	0.22	0.827

The final model was significantly different from the null model containing only group and individual as random effects (likelihood ratio test: n = 351, χ^2 = 33.88, $p < 0.001$, $R^2_{GLMM(c)}$ = 0.26). Male career stage was always compared to uninvested males as a reference category. Significant predictors are presented in bold and trends are italicized.

Table A2.7 Factors affecting the probability that males exhibited proactive aggression (proactive aggression without a female partner) during intergroup conflicts**,** after nonsignificant interaction terms were removed from the model.

Fixed Effects	***b* Estimate**	**SE**	***z***	***p***
(Intercept)	-2.18	3.26	-	-
Male career stage				
Uninvested males (reference category)	-	-	-	-
Dominant unlikely sire	1.78	1.47	1.21	0.226
Subordinate likely sire	**2.36**	**1.16**	**2.04**	**0.041**
Dominant likely sire	**2.51**	**1.16**	**2.16**	**0.031**
Residency				
Immigrant	-	-	-	-
Emigrant	-0.57	1.15	-0.50	0.619
Seasonal factors				
Month following first birth	0.78	0.92	0.86	0.392
Number of small infants	0.03	0.12	0.25	0.804
Seasonal habitat productivity	-1.81	3.09	-0.58	0.559
Mating season	-1.25	1.17	-1.07	0.283
Intensity of use	-0.06	0.31	-0.18	0.857
Distance to home range centre	-0.25	0.16	-1.61	0.108
Relative group size	0.02	0.09	0.20	0.838

The model failed to converge when the factor 'Immigrant' was included because recent immigrants were never seen to exhibit this type of aggression. The final model excluding 'Immigrant' was significantly different from the null model containing only group and individual as random effects (likelihood ratio test: $n = 351$, $\chi^2 = 41.00$, $p < 0.001$, $R^2_{GLMM(c)} = 0.50$). Male career stage was always compared to uninvested males as a reference category. The interaction between relative group size and the number of small infants was nonsignificant and was subsequently removed from the model ($n = 351$, $\chi^2_1 = 0.20$, $p = 0.657$). The model failed to converge when the interactions between male career stage and whether it was the month following the first birth of the season or not, male career stage and the number of small infants, male career stage and seasonal habitat productivity and male career stage and mating season were included; therefore, we could not evaluate the significance of these interactions. Significant predictors are presented in bold and trends are italicized.

Table A2.8 Factors affecting the probability that males supported female instigators during intergroup conflicts**,** after nonsignificant interaction terms were removed from the model.

Fixed Effects	***b* Estimate**	**SE**	***z***	***p***
(Intercept)	0.32	2.58	-	-
Male career stage				
Uninvested males (reference category)	-	-	-	-
Dominant unlikely sire	-4.00	2.53	-	-
Subordinate likely sire	0.24	1.78	-	-
Dominant likely sire	-2.65	2.01	-	-
Residency				
Immigrant	**-1.21**	**0.54**	**-2.23**	**0.026**
Emigrant	0.31	0.53	0.60	0.552
Seasonal factors				
Month following first birth	*1.43*	*0.86*	*1.66*	*0.098*
Number of small infants	-0.27	0.18	-1.52	0.129
Seasonal habitat productivity	-2.63	3.11	-	-
Mating season	**1.41**	**0.50**	**2.80**	**0.005**
Intensity of use	-0.30	0.22	-1.41	0.160
Distance to home range centre	0.07	0.07	0.94	0.349
Relative group size	0.06	0.06	1.04	0.299
Interactions				
Habitat productivity * Dominant unlikely sire	**11.69**	**5.09**	**2.30**	**0.022**
Habitat productivity * Subordinate likely sire	2.12	4.37	0.49	0.628
*Habitat productivity * Dominant likely sire*	*8.90*	*4.73*	*1.88*	*0.060*

The final model was significantly different from the null model containing only group and individual as random effects (likelihood ratio test: n = 340, χ^2 = 65.38, p < 0.001, $R^2_{GLMM(c)}$ = 0.38). Male career stage was always compared to uninvested males as a reference category. The removed nonsignificant interactions were those between male career stage and whether it was the month following the first birth of the season or not (n = 340, χ^2 = 1.00, p = 0.601), male career stage and the number of small infants in the group (n = 340, χ^2 = 1.46, p = 0.692), male career stage and mating season (n = 340, χ^2 = 4.23, p = 0.237) and relative group size and the number of small infants (n = 340, χ^2 = 0.00, p = 0.969). Significant predictors are presented in bold and trends are italicized.

Table A2.9 Factors affecting the probability that males supported female instigators during intergroup conflicts, with all dominant males pooled, regardless of their likelihood of paternity.

Fixed Effects	***b* Estimate**	**SE**	***z***	***p***
(Intercept)	0.31	2.59	-	-
Male career stage				
Uninvested males (reference category)	-	-	-	-
All dominant males (pooled)	-3.22	1.74	-	-
Subordinate likely sire	-0.15	1.76	-	-
Residency				
Immigrant	**-1.19**	**0.54**	**-2.22**	**0.026**
Emigrant	0.38	0.51	0.74	0.458
Seasonal factors				
Month following first birth	*1.48*	*0.86*	*1.74*	*0.083*
Number of small infants	-0.28	0.18	-1.56	0.118
Seasonal habitat productivity	-2.65	3.13	-	-
Mating season	**1.42**	**0.50**	**2.85**	**0.004**
Intensity of use	-0.31	0.22	-1.42	0.155
Distance to home range centre	0.07	0.07	1.03	0.303
Relative group size	0.05	0.06	0.84	0.403
Interactions	0.07	0.06	1.11	0.269
Habitat productivity * All dominant males	**10.24**	**4.03**	**2.54**	**0.011**
Habitat productivity * Subordinate likely sire	2.21	4.39	0.50	0.614

The final model was significantly different from the null model containing only group and individual as random effects (likelihood ratio test: n = 340, χ^2 = 65.10, p < 0.001, $R^2_{GLMM(c)}$ = 0.38). Male career stage was always compared to uninvested males as a reference category. Significant predictors are presented in bold and trends are italicized.

CHAPTER 3

Male food defence as a by-product of intersexual cooperation in a non-human primate

T. Jean M. Arseneau-Robar, Eliane Müller, Anouk L. Taucher, Carel P. van Schaik and Erik P. Willems

Males in a number of group-living species fight in intergroup conflicts to defend access to food resources, a seemingly paradoxical behaviour, given that this resource does not usually limit male fitness directly. We investigated the mechanism(s) driving apparent male food defence in wild vervet monkeys (*Chlorocebus aethiops pygerythrus*) by testing the effect that female resource access, and female audience size and activity had on the response of focal males during simulated intergroup encounters. Males do not appear to defend food to increase the reproductive success of female group members because their response was not influenced by the presence of provisioning boxes that only females could access. Female audience size was also unimportant, suggesting males do not participate in intergroup encounters to advertise their quality to potential mates. However, focal males almost always followed/supported female group members who initiated an approach towards simulated intruders, supporting that male participation largely functions to gain status as a cooperative group member, and that apparent male food defence in this species arises as a by-product of intersexual cooperation. Our study highlights that considering audience composition and activity can reveal the presence of social incentives and illuminate the evolutionary mechanism(s) promoting joint action in intergroup aggression.

Introduction

Although groups of many social species engage in aggressive intergroup conflicts with their neighbours (Boydston et al. 2001; Hölldobler 1981; Manson et al. 1991; Mares et al. 2012; Mosser and Packer 2009), in a number of species (including many primates), males are either the only sex that fights, or the sex that participates most actively (Goodall 1986; Scarry 2013; Sicotte 1993; Steenbeek 1999; Willems et al. 2013). In humans, males may gain both resource based and immaterial benefits from participating in intergroup conflicts (i.e. warfare) (Glowacki and Wrangham 2013; Wrangham and Glowacki 2012). Resource-based benefits are obtained from seizing valuable items from neighbouring groups, including food, mates and territory; conversely, immaterial benefits are social incentives that group members bestow on warriors (Glowacki and Wrangham 2013). For example, men who participate in intergroup conflicts may improve their status with group members, and as a result enjoy increased access to allies or wives (Glowacki and Wrangham 2013; Wrangham and Glowacki 2012). There is little evidence, however, that non-human animals use such social incentives to promote participation in intergroup conflicts, or in any other cooperative activity (Bergmüller et al. 2007; Wedekind and Milinski 2000).

In many non-human animals, males fight in intergroup conflicts to protect their offspring or defend access to mates (Boydston et al. 2001; Grinnell et al. 1995; Kitchen 2004; Kitchen and Beehner 2007), both of which could be considered resource-based benefits. There is also evidence for male food defence in some species (Arseneau et al. 2015; Fashing 2001; Harris 2010; Scarry 2013; Williams et al. 2004), but given that male fitness is primarily limited by access to receptive females (Trivers 1972) rather than food resources, this behaviour is

seemingly surprising. It is possible that males defend access to food resources to enhance the reproductive output of females and/or the survival of their offspring (Scarry 2013; Williams et al. 2004), or to attract more mates (resource defence polygyny; Emlen and Oring 1977). Alternatively, male food defence may simply arise as a by-product when males fight for other resource-based benefits (Willems and van Schaik 2015) or to gain social incentives. For example, while protecting their mates from harassment by extra-group males, males may end up defending food resources (the 'Hired Guns' hypothesis; Rubenstein 1986). Potential social incentives gained from food defence include social prestige, or building status as a cooperative group member. According to the social prestige hypothesis, males participate in high-risk and energetically costly intergroup conflicts to signal their genetic quality to potential mates (Zahavi 1975); females who choose to mate with the best fighters ensure their offspring will have these superior genes. The status building hypothesis proposes that because range defence is often a joint action, participation in intergroup conflicts is typically a cooperative activity; therefore, males may participate in intergroup conflicts to enhance their status as a 'good cooperative partner'. Given that food defence improves access to the resources that limit female fitness, doing so is most likely to enhance status with female group members rather than with males. If this is the case, apparent male food defence may be driven by mechanisms that promote intersexual cooperation (e.g. direct and/or indirect reciprocity mechanisms (Alexander 1987; Axelrod and Hamilton 1981; Nowak and Sigmund 1998; Trivers 1971)). For example, a number of studies have found evidence that direct reciprocity can promote cooperative behaviour in primates, and that various services are often traded (e.g. tolerance, grooming, support in agonistic interactions, food sharing and sex) (Borgeaud and Bshary 2015; de Waal 1997; Gumert 2007; Koyama et al. 2006; Seyfarth and Cheney 1984; Tiddi et al. 2011; Ventura et al. 2006). It is possible that defending resources that limit female fitness is a service that males trade with females. In return, females may also provide a variety of services, but when females are able to exert choice in mating partners, sex is the most valuable commodity with obvious fitness benefits for males who are preferred partners.

A recent study on intergroup aggression in vervet monkeys (*Chlorocebus aethiops pygerythrus*) found apparent evidence for male food defence (Arseneau et al. 2015), but the mechanism(s) that drive this behaviour are unclear. As noted above, male food defence possibly serves to increase female reproductive success, to gain social prestige, to build status as a cooperative group member, or males may simply be acting as 'Hired Guns'. All these functions are possible in vervet monkeys and the four mechanisms are not mutually exclusive. Vervet monkeys live in multi-male multi-female groups in which females are philopatric and males disperse multiple times throughout their lives, starting at sexual maturity (Cheney and Seyfarth 1983). Parallel dispersal of males does occur (Cheney and Seyfarth 1983), but it is not common. Therefore, adult males are unrelated to their female group members, and also usually unrelated to each other. Males are approximately 1.5 times larger than females, yet both sexes participate actively in intergroup conflicts (Arseneau et al. 2015). Females often instigate intergroup aggression and males frequently support them when they do so (Arseneau

et al. 2015). Both sexes direct aggression at both male and female members of opposing groups (Arseneau et al. 2015; Cheney 1987). Because the 'Hired Guns' hypothesis predicts that food defence arises only as a by-product of male-male competition over mates, and male intergroup aggression is often targeted at females (Arseneau et al. 2015; Cheney 1981), the 'Hired Guns' function is unlikely in this species. However, larger vervet groups tend to have higher-quality home ranges and experience slightly higher infant survival (Cheney and Seyfarth 1987), indicating that greater resource availability could potentially increase female reproductive success. Female vervet monkeys are able to refuse matings (i.e. exert mate choice) and are highly promiscuous, mating with multiple male group members (Arseneau et al. 2015; Struhsaker 1967). Mating skew is low with two or three males typically gaining a high proportion of matings each year, and male mating success correlates with their propensity to participate in intergroup conflicts (Arseneau et al. 2015). As such, apparent male food defence could be a by-product, produced as males signal their genetic quality to female group members. Alternatively, this correlation could equally mean that apparent male food defence is a by-product of mechanisms that promote intersexual cooperation, for example, that males trade support in intergroup conflicts for sex. Recent experimental work in vervet monkeys demonstrates that females trade grooming for tolerance and support in intragroup conflicts (Borgeaud and Bshary 2015), indicating that a reciprocity-type mechanism could potentially function to promote intersexual cooperation as well.

To elucidate which mechanism(s) underlie apparent male food defence in a wild population of vervet monkeys, we took an experimental approach in which we used playbacks to simulate the presence of a neighbouring group nearby when females had, or did not have, access to provisioning boxes (i.e. a high-quality food resource). Provisioning boxes contained slices of apple with two pieces of corn imbedded in them, and were operated by observers such that access was restricted to female group members. During all playback trials we recorded the response of focal males, as well as the composition of their audience and the response of audience members to the simulated intruders. If males defend food resources to increase female reproductive success, then males should exhibit the strongest response to simulated intruders when females had access to high-quality resources, and their response should be independent of the composition and/or response of audience members. If males participate in intergroup conflicts to gain social prestige, then the size of the female audience (i.e. number of potential future mates) present to observe the honest and costly signal should have the strongest influence on the response of males. Conversely, if apparent food defence is a by-product of intersexual cooperation, then the response of males should be most influenced by the presence of a cooperative partner. Therefore, if a female group member instigates an approach towards the simulated intruders, then focal males should follow and support them.

Methods

Field Experiments

Data were collected on three habituated groups of vervet monkeys at the Mawana Game Reserve (28°00'S, 31°12'E) in South Africa. Groups consisted of 30 to 56 individuals, with between one and seven adult males and five and 14 adult females. We first trained individuals on the provisioning boxes between May 2012 and July 2013. The goal of training was for females to learn that the boxes contained high-quality food resources they could access, and for males to learn that because the boxes were opened only for females, they were excluded from accessing the high-quality resources within. Male exclusion ensured that males understood they would gain no direct personal benefit from defending provisioning boxes against simulated intruders so that if males did defend the provisioning boxes during playback experiments, they did not do so to increase their own food intake.

In each training session, we deployed six boxes and allowed females to access them until they lost interest. During the summer, when high-quality foods were available in the environment, females were often not interested in the boxes. During the winter, when food resources were scarce, females interacted with the provisioning boxes for 75 minutes on average. Boxes were provisioned with apple wedges embedded with two pieces of corn. All boxes were opened simultaneously to ensure that high-ranking females could not displace low-ranking females from a box. Each time the boxes were opened, researchers played a particular audible sound effect (of a musical instrument) so that group members who were out-of-sight of the provisioning boxes would be aware that females were accessing the high-quality resources.

On average, males experienced 14 training sessions before the playback experiments commenced. During each training session, we recorded the number of box openings in which males attempted to gain access to the food within the provisioning boxes. When males stopped trying to open the provisioning boxes, this was taken to indicate that they had learned that they were excluded from access. Some of the males quickly learned exclusion and no longer attempted to gain access to the boxes (Figure 3.1); however, other males would still test if they were able to access the boxes at the start of most training sessions. However, by the end of the training period, these males typically "gave up" and moved away from the boxes after they had observed females feeding, and saw that they were excluded, for one opening of the boxes (the maximum number of openings before giving up was 3). Once they had left (>5 m up into the tree canopy or out of sight of the provisioning boxes' location) they never returned to attempt accessing the provisioning boxes again. Therefore, when we conducted playback trials in which females had access to high-quality resources, we always set up the provisioning boxes and allowed females to access them for ~30 minutes before conducting the playback experiment. This ensured that males who would test their access/exclusion could do so. If a male did attempt to access a provisioning box, we waited for him to move more than 5 m away from the boxes, and

maintain that buffer distance for at least 10 minutes. We took this to indicate that he understood he would not gain any direct personal benefits from defending the provisioning boxes against simulated intruders.

Playback experiments were conducted in the dry season (July to November 2013) when naturally occurring fruits and seeds were scarce and females were most interested in the provisioning boxes. This period included the latter half of the mating season, the time of gestation and the beginning of the birth season. The playback stimulus consisted of a female-female conflict (recorded in a feeding context), followed 30 seconds later by a chorus contact call, which is the vocalization typically made by females during intergroup encounters. Vocalizations were recorded using a Marantz Professional solid state Recorder PMD 660 with a directional Sennheisser MKH416P48U microphone. The amplitude of stimuli was standardized (Audacity 2.0.3) so that all vocalizations sounded natural to experienced observers at 65-90 m. In each playback trial, the speaker (MiniVox Lite, Anchor Audio Ltd.) was placed so that the stimulus came from a location that was credible for the group being broadcast. The speaker was placed 65 to 90 m away from the focal individuals to ensure that the stimulus was audible but that the observer playing the stimulus was not visible. All playback experiments were conducted in areas that were used intensively by the focal group to decrease the potentially confounding effect of location(Crofoot and Gilby 2012). In playback trials performed in conjunction with the provisioning boxes, the stimulus was played approximately 30 minutes after the boxes were first presented.

We recorded the response of one to three focal males (as well as one or more females) using handheld and time-synchronized camcorders. In each group we focal sampled both dominant and subordinate males; the number of subordinate males that were focalled varied from one to four, depending on the number of male group members and the occurrence of male immigration/emigration events. We attempted to sample focal males within each group at equal frequencies, however, this was not possible as some males immigrated/emigrated during the study period. Additionally, focal males typically needed to be near the front of the group to be within the 65 to 90 m range from the speaker, and not all males were equally likely to be in this position in the group. As a result, the number of trials per male varied from one to three in group A, one to five in group B and six to eight in group C. Focal males were usually not part of the same subgroup, and as such, were only in visible range of each other during three experimental trials (see Results section).

For each focal individual we noted the number, identity, and location (relative to the focal) of all visible group members (i.e. the audience) just prior to playing the stimulus. This ensured that when analyzing the video, we were able to determine which audience members the focal male looked at during the experiment. Once the stimulus was played back, each observer recorded the response his/her focal male, whilst speaking to the camera, noting if and when the focal moved more than 5 m from their initial location, and which visible neighbours vocalized and/or moved. The observer at the speaker also noted if and when any individuals approached the speaker. Video recordings and recorded notes from all observers present were pieced

together for each trial to create a comprehensive picture of which group members vocalized and/or approached the speaker, and the exact time they did so; with these data, we were able to determine if focal males either followed, led or ignored group members.

Focal individuals were scored as approaching if their initial response was to move at least 5 m towards the speaker during the trial (i.e. within five minutes of the stimulus) (Crofoot and Gilby 2012; Kitchen 2004). Focal males were scored as following a female leader if this approached occurred after one or more female group members who were visible to the focal had already begun to approach the speaker (usually while vocalizing). Female vervet monkeys often initiate intergroup conflicts (Arseneau et al. 2015), and to recruit support they begin to approach the opposing group while vocalizing and being vigilant. Group members who approach instigator females signal a willingness to support them and engage in an intergroup encounter. Thus, an approach was considered to indicate the willingness of the focal male to participate in an intergroup encounter.

Statistical Analyses

We used a generalized linear mixed model (GLMM) to test if males were more likely to approach the simulated intruders when females had, versus did not have, access to high-quality food resources (provisioning boxes). We also tested the importance of male rank, the size of the female audience, and the presence of a visible female leader by including these three terms as predictor variables in the model. Because the response variable was binary, we set a binomial error structure and fit a logit link function in the model. To control for repeated observations we included the trial number, as well as the focal individual nested within group as crossed random effects (Zuur et al. 2009). We based our inferences on the full model rather than using a stepwise procedure to avoid false positives and biased effect size estimates (Forstmeier and Schielzeth 2011). All statistical analyses were conducted in R (version 3.0.3) (R Core Team 2014) using the lme4 package (Bates et al. 2015).

Ethical Considerations

The experimental protocol approved by the Ezemvelo KZN Wildlife Board in South Africa and field experiments were carried out in accordance with the relevant guidelines and regulations. In addition, we took numerous steps to ensure that our experiment had a minimal effect on the behaviour of our study subjects. Because the study site is a large private game farm used for hunting (as opposed to crop farming), there was little risk that introducing the study subjects to corn in the experiment could dispose them to crop raiding. Moreover, to ensure that provisioning did not dispose the study subjects to becoming human food stealers, we trained the monkeys to only expect food in a highly specific set of conditions; if these conditions were not met, the study

subjects never showed any sign that they expected humans to provide them with food. First, all researchers wore blue hats in the field. Second, on days when only observational data were collected, researchers always made "habituation" calls as they approached the study group; conversely, on days when experiments that included provisioning occurred, researchers made an alternative "food" call as they approached. Third, food was always provisioned via an experimental box (which were decorated so as to be distinct and unique), and was never given directly from a researcher to a monkey.

Results

We conducted a total of 24 playback experiments in three wild groups of vervet monkeys. During playback experiments, the presence of an intruding group was simulated and the response of one to three focal males was recorded. In 12 of these playback trials, females had access to provisioning boxes that were a source of high-quality food resources, and in the remaining 12 trials, no provisioning boxes were present. Focal males had previously been trained to learn that provisioning boxes could only be accessed by female group members, and therefore, that they would personally gain no resource-based benefit from defending them. Males typically responded to the playback stimulus by orienting their bodies towards the speaker and so we did not include any trials in which the focal male did not acknowledge the playback stimulus in this manner in our analyses. Males usually remained vigilant towards the simulated intruders for five to 10 seconds before beginning to monitor the behaviour of their group members. In some cases, males began to approach the speaker soon after checking on their group members, while in other cases they monitored the behaviour of their group members for many minutes before approaching.

We found that dominant males were no more likely to approach the simulated intruders than subordinate males (GLMM: $b \pm SE = 0.44 \pm 1.10$, $z = 0.40$, $n = 34$, $p = 0.692$; Figure 3.2a). Similarly, males were no more likely to approach the speaker when females were accessing high-quality food resources than when there were no provisioning boxes present ($b \pm SE = 1.14 \pm 1.22$, $z = 0.94$, $n = 34$, $p = 0.349$; Figure 3.2b). The presence of a large female audience at the time the stimulus was played also had no significant effect on the response of focal males ($b \pm SE = -0.47 \pm 0.58$, $z = -0.81$, $n = 34$, $p = 0.421$; Figure 3.2c). However, the presence of a female leader had a strong and highly significant effect on the tendency for males to approach simulated intruders ($b \pm SE = 4.73 \pm 1.81$, $z = 2.62$, $n = 34$, $p = 0.009$; Figure 3.2d). In fact, the odds ratio (calculated from the raw data) indicates that males were 35 times more likely to approach the playback stimulus when a female group member began to vocalize and approach the speaker first. In only one of the observed cases in which a female leader was present, did the focal male ignore (rather than follow and support) her. In all cases where the focal male followed a female leader, only a single female needed to vocalize and approach the speaker before the male followed; therefore, we were unable to consider the effect that the number of female leaders

had on the propensity of males to approach the simulated intruders. In only three trials did the focal male have another male in his audience, and in none of these cases did either male approach the simulated intruders. Thus, although we lacked the data for a formal investigation of the effect of male audience members, the presence of another male, or potential cooperative partner, appears to have had little effect on the response of focal males during playback experiments. Notably, there was also not a visible female leader in any of these three cases.

Discussion

Male food defence is a seemingly puzzling behaviour given that food is not the primary resource that limits male fitness. Male food defence in vervet monkeys potentially functions to increase female reproductive success and increase male fitness indirectly, build social prestige, or improves status as a good cooperative partner. To test these three hypotheses, we employed a novel experimental approach in which we manipulated male and female access to high-quality resources and simulated an intruding group nearby. These experiments were conducted in a season when naturally occurring resources were scarce and females were gestating; thus, male food defence in this season could have a large impact on the reproductive success of female group members. However, males showed no greater tendency to engage in an intergroup encounter when females had exclusive access to high-quality food resources, than when they did not. Therefore, our results are inconsistent with the hypothesis that males defend food to improve female reproductive success in this species. This mechanism is most likely to function in territorial species where males are the philopatric sex, as these are the conditions in which the benefits of improving resource access for females could accrue over long time periods (e.g. chimpanzees) (Williams et al. 2004).

It has also been suggested that males may defend food to improve female reproductive success, even when they are the dispersing sex and their tenure in a given group is relatively short (Scarry 2013). However, despite the potential indirect fitness benefits, males may fail to defend food resources on behalf of females as doing so is vulnerable to the free-rider problem (Hardin 1968; Olson 1965). In vervet monkeys for example, females are highly promiscuous, mating with multiple male group members throughout the mating season (Struhsaker 1967); all male group members obtain at least some matings, and mating skew is often relatively low among males (Arseneau et al. 2015). As a result, males who would defend food resources to indirectly increase their fitness would also provide similar benefits to their fellow male group members. Males who refrain from food defence would gain indirect fitness benefits without paying any cost, and selection would favor a defection strategy. This strategy of male food defence for indirect fitness benefits is therefore unlikely to evolve unless reproductive skew is high or males are close relatives. Neither condition applies to vervet monkeys (Struhsaker 1967).

If male participation in intergroup conflicts functioned as a costly signal, we would expect males to show the strongest response to simulated intruders when there was a large audience of females (i.e. many potential future mates) to observe them. However, despite the fact that many of our playbacks occurred during the mating season, we found no effect of female audience size on the likelihood that males approached the speaker, suggesting that males do not use intergroup encounters as an opportunity to advertise their genetic quality to females (Zahavi 1975). Instead, we found that the response of males was highly dependent on the behaviour of female audience members during playback experiments. Males rarely led the approach towards simulated intruders, suggesting that it is unlikely that they were motivated by resource-based benefits. Conversely, if female group member(s) instigated an approach then males almost always followed and supported them, which supports that male participation in intergroup conflicts largely functions as intersexual cooperation. Therefore, apparent male food defence appears to be a by-product, arising from the combination of female food defence and intersexual cooperation. Previous work on our study population found that approximately a third of the variability in male mating success was related to the frequency with which males supported females in intergroup conflicts (Arseneau et al. 2015), indicating there are tangible fitness benefits associated with being a cooperative group member. Future studies are necessary to determine the precise evolutionary mechanism(s) by which males build their status as a cooperative group member (e.g. direct reciprocity and/or indirect reciprocity).

Support during intergroup encounters is likely only one of many services that males provide in this species, with other potential services including predator vigilance and mobbing, coalitionary support in intragroup conflicts, tolerance around valuable food resources and grooming. Furthermore, such male services are likely more widespread among social animals than is generally appreciated, and may thus represent an important proportion of cases of male assistance in primates, other mammals, and birds. An interesting avenue of future investigation lies in understanding how the amount of choice that females are able to exert in their mating partners influences the extent and type of male services observed.

Our findings highlight that when intergroup aggression is a cooperative activity involving the joint action of multiple individuals, who an individual participates in aggressive intergroup interactions with can be more important than the resources they end up defending. Therefore, it is important to investigate both the resource-based benefits and social incentives gained from participation in intergroup aggression, and considering both the ecological and social contexts in which individuals participate is critical to doing so. Examining audience effects is a useful approach as the makeup of the audience (e.g. the number of individuals, their sex, relationships and reproductive status) as well as their activity (e.g. whether they are active or not, and who leads versus follows) can illuminate the role that social incentives play in the evolution and maintenance of cooperation (Heinsohn and Packer 1995; Meunier et al. 2012).

Chapter 3 Figures

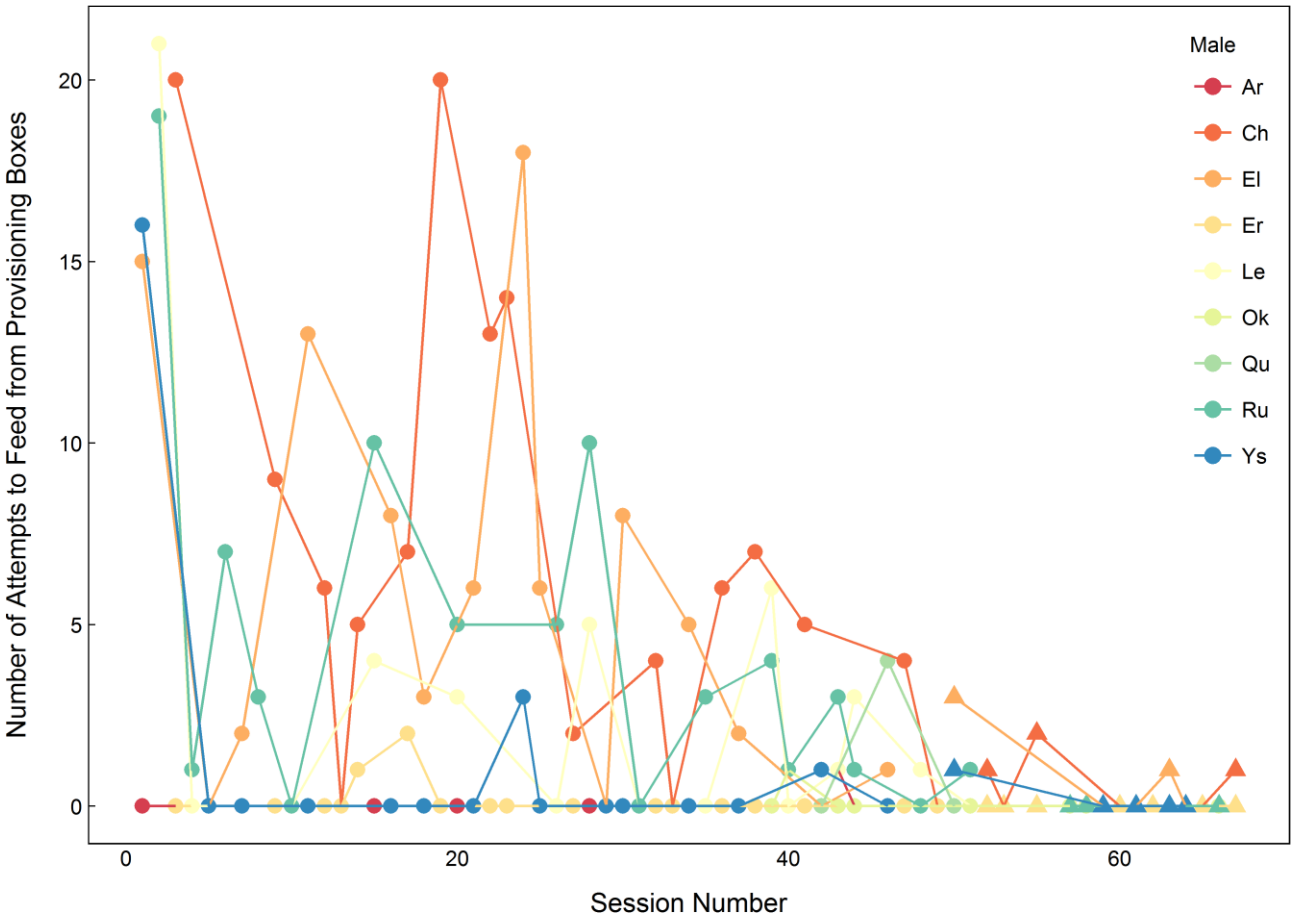

Figure 3.1 Number of attempts that each male made to access the female-only provisioning boxes. Circles represent training sessions before playback experiments commenced, triangles represent sessions after playback experiments started.

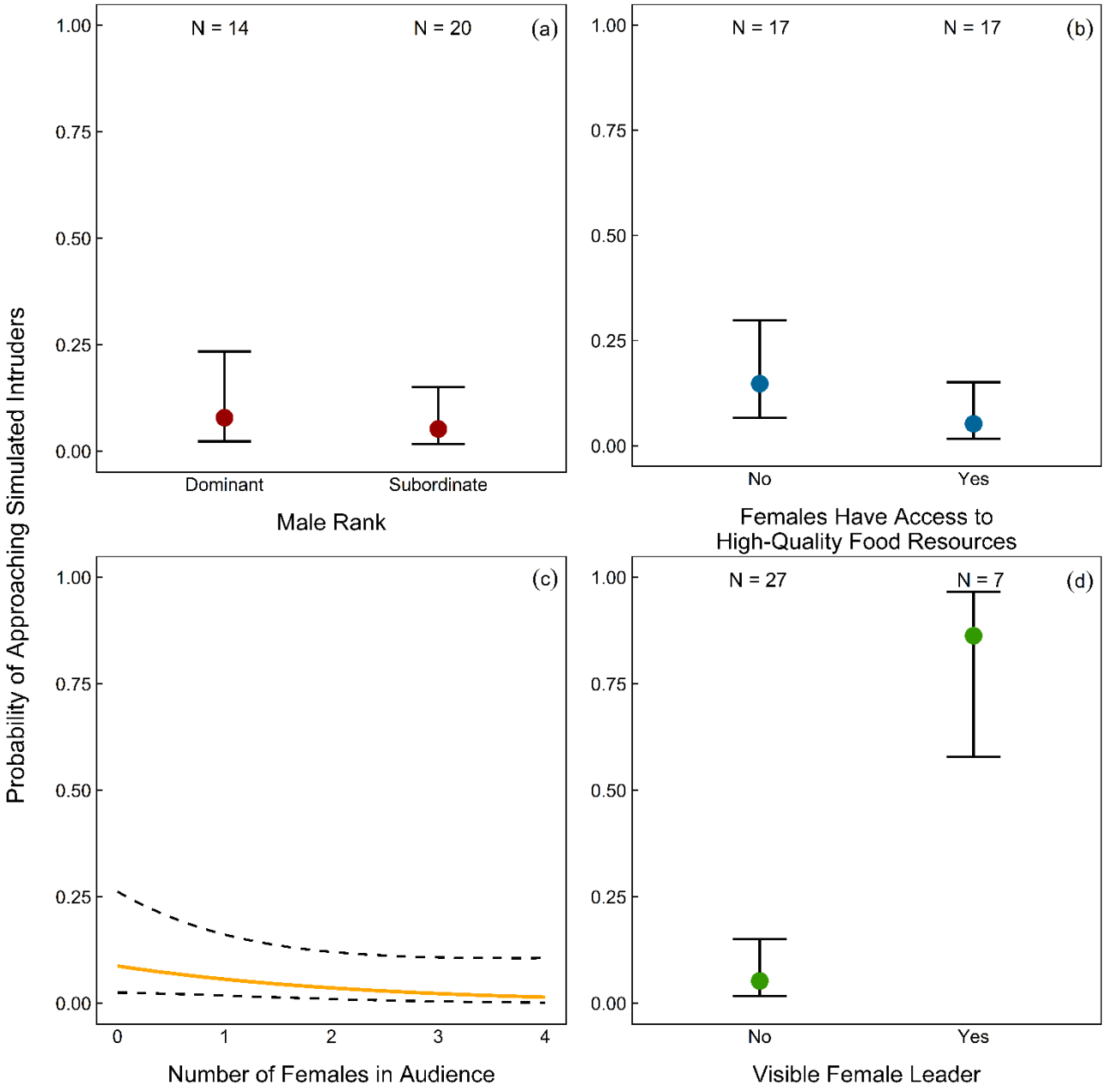

Figure 3.2 Probability that males approached the speaker during playback experiments, depending on (a) their rank, (b) whether female group members did versus did not have access to provisioned resources (c) the number of females in their audience, and (d) whether or not a female group member led an approach first. Predicted values and predicted standard errors (error bars and dotted lines) were obtained by setting all additional factors in the GLMM model to their mean (or median for binary variables) value.

CHAPTER 4

Female monkeys use punishment and rewards to promote male participation in intergroup conflicts

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Group-level cooperation often poses a social dilemma in which joint action may be difficult to achieve. Theoretical models and experimental work on humans show that social incentives, such as punishment of defectors and rewarding of cooperators, can promote cooperation in groups of unrelated individuals. Here, we demonstrate that these processes can operate in a non-human animal species, and be used to effectively promote the production of a public good. We took advantage of the fact that intergroup conflicts in vervet monkeys (*Chlorocebus aethiops pygerythrus*) are characterised by episodes of intergroup aggression with pauses in-between. During pauses, females selectively groomed males that had participated in the previous aggressive episode, but aggressed male group members that had not. In subsequent (i.e. future) episodes, males who had received either aggression or grooming participated above their personal base-line level. Therefore, female-male aggression and grooming both appear to function as social incentives that effectively promote male participation in intergroup conflicts. Importantly, females stood to gain much from recruiting males as the probability of winning intergroup conflicts was dependent on the number of active participants, relative to the number of fighters in the opposing group. Furthermore, females appear to maximise the benefits gained from recruiting males as they primarily used social incentives where and when high-quality food resources, which are the resources primarily limiting to female fitness, were at stake.

Introduction

Helping among unrelated individuals has attracted major research efforts among evolutionarily minded scientists as it has to be reconciled with a theory that strongly emphasises competition (Clutton-Brock 2009; Dugatkin 2002; Hardin 1968; Maynard Smith 1982; Olson 1965; Rand and Nowak 2013; West et al. 2007). In group-living species, actions like predator vigilance, cooperative hunting, or the defence of territories often produce a public good, where individuals that do not contribute receive greater payoffs than those that do. The former are called free-riders or defectors while the latter are called cooperators. Thus, group-level cooperation often poses a social dilemma in which cooperators, who contribute to the production of the public good, are vulnerable to exploitation by their free-riding group members (Olson 1965). Such dilemmas are often modelled as an n-player Prisoner's Dilemma, where the self-serving decision of individual group members is to defect, even if this does not result in the maximum possible pay-off at the level of the group (Hamburger 1973; Tucker 1950). However, many social dilemmas in nature may better fit the framework of a Volunteer's Dilemma (an n-player Snowdrift), in which individuals still prefer to free-ride, unless not enough cooperators are present to secure the production of the public good, in which case cooperation becomes the self-serving strategy (despite a certain degree of exploitation) (Archetti 2009; Diekmann 1985). Besides such negative frequency dependencies in a Volunteer's Dilemmas, spatial population structure and social incentives can also favour contributions to public goods based on direct fitness benefits (Archetti and Scheuring 2011; Glowacki

and Wrangham 2013; Kandori 1992; Milinski et al. 2002; Sherratt et al. 2009; Willems et al. 2015). For example, public goods experiments conducted on humans in a laboratory setting show that social incentives like the punishment of defectors and rewarding of cooperators can effectively promote cooperative behaviour (Fehr and Gächter 2000; Sefton et al. 2007).

One of the riskiest joint actions that humans engage in is warfare, and social incentives are thought to have been important in promoting the participation (i.e. cooperation) of male warriors in primitive warfare (Boyd et al. 2010; Glowacki and Wrangham 2013; Mathew and Boyd 2011). The majority of animal species, however, do not engage in warfare (Aureli et al. 2006; Goodall 1986) but group members still cooperatively defend a territory, or parts of their home range. Cooperative intergroup aggression in non-warring animals is nevertheless a high-risk activity, potentially resulting in injury or death (Cant et al. 2002; Cheney and Seyfarth 1987; Gros-Louis et al. 2003; Kruuk 1972; Mech 1994; Mosser and Packer 2009), and is prone to social dilemmas (e.g. the collective action problem (Nunn and Deaner 2004; Nunn and Lewis 2001; Olson 1965; Willems et al. 2013; Willems and van Schaik 2015)). Unlike in humans, there is little empirical evidence that animals use social incentives to manipulate the participation of their group members and overcome social dilemmas during intergroup conflicts. In fact, studies clearly demonstrating that non-human animals use punishment or rewards to manipulate the cooperative behaviour of conspecifics in any context are remarkably limited (Raihani et al. 2010; Raihani et al. 2012b).

We conducted a field study of intergroup aggression in vervet monkeys (*Chlorocebus aethiops pygerythrus*), a species in which both sexes participate aggressively during intergroup conflicts, even though males are approximately 1.5 times larger than females (Arseneau et al. 2015; Cheney 1981). Patterns of intergroup aggression in this species follow the predictions of the Volunteer's Dilemma, in which the payoffs of home range defence are non-linear (Archetti 2009; Diekmann 1985). That is to say, production of the public good (i.e. home range defence) does not increase linearly with the number of participants, rather a certain number of volunteers are required to successfully secure the public good (Archetti 2009; Diekmann 1985). In vervet monkeys, typically only a small proportion of group members participate in a given intergroup conflict, and although individual participation is highly variable, the average number of individuals who participate in intergroup conflicts is similar among groups (Willems et al. 2015). Given that defending access to food resources can have significant fitness benefits for female primates (Lee and Hauser 1998; Robinson 1988; Takahata et al. 2006; Takahata et al. 1998; Williams et al. 2004), females likely have a strong incentive to participate in intergroup conflicts when valuable food resources are at stake. Furthermore, because they are the philopatric sex, female vervet monkeys stand to gain long-term direct and indirect fitness benefits from effective home range defence (Cheney and Seyfarth 1987; Isbell et al. 1990). However, high-ranking females are more likely to participate in intergroup conflicts and low-ranking individuals are more likely to free-ride on

the efforts of others (Cheney 1981; Willems et al. 2015), which suggests that those who have priority of access to defended resources are those most likely to volunteer. Male vervet monkeys migrate repeatedly during their lives, residing in a group for a few months or a few years. Because food is not a key resource limiting male fitness, males are not expected to contribute to food defence (Trivers 1972). Instead, male vervet monkeys participate in intergroup conflicts for one of two benefits (Arseneau et al. 2015). First, males who are likely to have sired offspring react defensively when members of the opposing group are highly aggressive, such that offspring may be at risk (Arseneau et al. 2015). Second, males also support females in instigating intergroup aggression, however, this primarily occurs during the mating season when doing so is associated with higher mating success (Arseneau et al. 2015). As a result, females may receive little support from their larger-bodied male group members for much of the year, including much of the summer season when high-quality food resources are at stake. If recruiting more active participants increases the likelihood of winning access to food resources, females potentially have a strong incentive to manipulate the participation of male group members to increase the fighting ability of their group. In social species, competitive ability is typically thought to increase with group size (Mosser and Packer 2009; Williams et al. 2004) but numerous studies have shown that smaller groups frequently win intergroup conflicts (Bonanni et al. 2010; Crofoot et al. 2008; Robinson 1988; Sugiura et al. 2000; Zhao and Tan 2010). When individual participation is highly variable, larger groups can suffer defeat if defection among group members is high (Crofoot and Gilby 2012; Crofoot et al. 2008). Therefore, the relative number of active participants, rather than relative group size, may determine the outcome of intergroup conflicts (Zhao and Tan 2010). Given that only a proportion of group members typically participate in a given intergroup conflict and individual participation is highly variable in vervet monkeys (Arseneau et al. 2015; Cheney 1981; Willems et al. 2015), it is very likely that the relative number of active participants determines who wins intergroup conflicts in this species.

Intergroup conflicts were comprised of discrete episodes of intergroup aggression, with periods of calm in-between. Typically, aggressive episodes consisted of one or more individuals running towards the opposing group while making aggressive vocalisations, or chasing an individual from the opposing group. During calm periods, or pauses, in which the two groups were in close proximity but not interacting, we observed female actors directing social behaviours towards adult males from their own group. These social behaviours could be either affiliative (i.e. grooming) or aggressive; female-male aggression (FM-agg) typically started with female actor(s) vocalising and making a threatening display towards a target male who was within a couple of meters. These displays often escalated into a chase, and in a couple of instances the female actors physically attacked the target male. These social behaviours typically occurred when the actor and target were near the front-line, monitoring the opposing group. Thus, FM-agg and female-male grooming (FM-gr) appear to relate directly to the context of the intergroup conflict rather than an alternative context such as feeding. Here, we

investigate whether these social behaviours potentially function as social incentives, used by females to manipulate the participation of male group members in future aggressive episodes.

To ascertain if FM-agg and FM-gr function as social incentives, we first test if females benefit from manipulating male participation in intergroup conflicts by examining the effect that the number of aggressive participants had on the odds of winning. Then, we investigate the spatio-temporal variability in the occurrence of these social behaviours. If females use aggression and grooming to manipulate males in defending resources that limit female fitness, females should be more likely to exhibit these behaviours during time periods, and in locations where valuable food resources are at stake. Lastly, we test if FM-agg functions as punishment for defection, and if FM-gr functions as a reward for participation. If this is the case, females who attempt to solicit male support should direct aggression towards males who did not participate in the most recent aggressive episode, but groom males who did. Furthermore, males who receive FM-agg should become more likely to participate in subsequent aggressive episodes (Clutton-Brock and Parker 1995), and males who receive FM-gr should maintain elevated levels of participation.

Methods

Study Subjects and Study Site

Data were collected on four habituated groups of vervet monkeys at the Mawana Game Reserve (28°00'S, 31°12'E), South Africa, with all data collection protocols approved by the appropriate local authority, the Ezemvelo KZN Wildlife Board. Vervet monkeys live in multi-male multi-female groups, in which females are the philopatric sex and males emigrate multiple times throughout their adult lives. At this study site, groups consisted of one to seven males and five to 14 females. All animals in the four focal groups were individually recognised, as were most of the adults in the neighbouring and frequently encountered groups.

Behavioural Data Collection

We conducted one to two days of observational data collection on each group, each week, for a total of >11000 observation hours during the study period (January 2012 and February 2014). On these days we performed group scans every 30 minutes, and also recorded all observed social interactions (i.e. all-occurrence data). For each social interaction, we recorded the context (e.g. feeding, social), actor and recipient, and whether the actor received support from any group members.

Participation during intergroup encounters was also collected on an all-occurrence basis and encounters were deemed intergroup conflicts when one or more individuals from either group exhibited intergroup aggression. During aggressive episodes, participants could direct intergroup aggression towards the opposing group as a

whole (e.g. run towards the group making aggressive vocalisations), or aggress specific individuals (e.g. chase, grab or bite a member of the opposing group). Throughout each intergroup conflict, we recorded the time that each aggressive episode was instigated, the identity of active individuals, behaviour(s) exhibited, and the identity of the individuals intergroup aggression was directed towards. We recorded the same information when there was a social interaction within the group. One group was deemed to have won an intergroup encounter if they displaced the opposing group from the contested location. When the two groups tolerated each other until one group left the area, the encounter was categorised as having no clear winner (i.e. a draw).

We used this dataset to determine if targeted males had participated in the last aggressive episode prior to, as well as the next aggressive episode following FM-agg or FM-gr. However, we observed both FM-agg and FM-gr before any intergroup aggression had been exhibited (n = 22), in the middle of intergroup conflicts (n = 39), as well as just before the opposing group retreated and the intergroup conflict ended (n = 10). Additionally, there were cases where the participants of aggressive episodes, female actors, or male targets, were not identified (although their age class/sex was determined). Therefore, our analyses were typically based on a subset of data in which an aggressive episode had occurred (before or after the social incentive, depending on the analysis) and the identity and behaviour of the relevant actors/targets/participants was known. We report the sample size that each analysis was based on.

Statistical Analyses

To examine the spatio-temporal variability in the occurrence of FM-agg and FM-gr, we used a generalised linear mixed model (GLMM), in which the dependent variable was whether or not either of these social incentives were observed in a given intergroup encounter. We set group as a random effect, a binomial error structure and a logit link function, and included four fixed effects. The three seasonal fixed effects included were the birth season (October to December), the summer season (November to May), and the mating season (April to July). The birth season was indexed by the number of small infants (less than three months old) in the group, and the summer season was indexed using monthly average normalised difference vegetation index values (NDVI), which correlates with field measurements of food availability and shelter in vervet monkeys (Willems et al. 2009) (see Chapter 4 Appendix for further detail). To account for the spatial variability in food resources, the last fixed effect we included in the GLMM was the relative availability of fruits in the area in which the intergroup conflict took place, compared to what was available in the rest of the home range (see Chapter 4 Appendix for further detail).

A Fisher's exact test was used to test if when using social incentives, females directed aggression towards males who had recently defected and grooming towards males who had recently participated. We then examined the effect that FM-agg and FM-gr subsequently had on the cooperative behaviour of males both at

the population level, and the individual level. At the population level, all observations of punishment (or rewards) were pooled and the identity of the target male was not considered; at the individual level, the propensity to participate before versus after receiving punishment (or rewards) was determined for each male in the population. The former was tested using a Chi-squared test, and the latter using a Wilcoxon signed ranks test. We further examined the effect that social incentives had on male participation by comparing the proportion of aggressive episodes in which males participated following FM-agg (or FM-gr), to their individual base-line level of participation (i.e. the proportion of episodes participated in during intergroup conflicts in which social incentives were observed, but they were not the male targeted). We used a Chi-squared test to determine if groups with more active individuals were more likely to win intergroup conflicts, as well as if males were more likely to be the target of female aggression (and female grooming) during intergroup conflicts than in other contexts.

In order to assess the magnitude of effects for all of our analyses (Garamszegi et al. 2009; Nuzzo 2014), we present the appropriate effect size statistics: odds ratio with Chi-squared tests, r with Wilcoxon signed rank tests and $R^2_{GLMM(c)}$ in our GLMM (Field et al. 2012; Nakagawa and Schielzeth 2013). The overall significance of the GLMM model was assessed by comparing the final model to the null model (model including intercept and random effect only) using a likelihood ratio test. In all analyses, α was set at 0.05, but we also discuss non-significant trends ($0.05 < p < 0.10$) when they are biologically interesting. All statistical analyses were conducted in R (version 3.0.3, R Core Team 2014) and we used the lme4 package (version 1.1-4, Bates et al. 2015) to fit the GLMM model.

Results

During more than two years of observation of four habituated groups of vervet monkeys, we observed more than 400 intergroup encounters, approximately half of which (n = 236) escalated into an intergroup conflict. Intergroup conflicts were 45 minutes long on average, but could be extremely brief or last up to eight hours (mean ± SD = 45 ± 55 min., range = 1 to 475 min.). A third of intergroup conflicts consisted of a single episode of intergroup aggression, but the majority of intergroup conflicts were prolonged, consisting of multiple aggressive episodes (mean ± SD = 4.6 ± 3.0 episodes; range = 0 (only the opposing group exhibited intergroup aggression) to 15 episodes) that were typically spaced three to four minutes apart. However, when neither group was able to displace the other, the two groups often gave up fighting and tolerated each other nearby. In such situations, the pause between aggressive episodes could last up to three hours before members of either group re-initiated an intergroup conflict.

It was typically only a small proportion of group members that participated in each aggressive episode, with the average number of active males being 0.7 (SD = 0.7; range = 0 to 3), and the average number of female

participants being 1.4 (SD = 1.5; range = 0 to 7). Thus, male support was absent in approximately half of the observed aggressive episodes, and it was rare that there was more than one male active at the front-line (fewer than 10% of aggressive episodes). We observed significant interindividual variability in male participation (in intergroup conflicts where no FM-agg or FM-gr were observed), with some males never being observed participating, and the most active males in ~55% of the episodes they experienced (mean ± SD = 22 ± 17%; Figure 4.1).

Benefits of Recruiting Males

The number of adult participants varied greatly among intergroup conflicts; in some cases no group members exhibited intergroup aggression (i.e. the group avoided or fled from a confrontation), while in other intergroup conflicts, up to 60% of adults were active participants. As would be expected when individual participation is so highly variable, it was the relative number of active participants throughout the intergroup conflict that determined which group was able to displace the other from the contested location. The odds ratio indicates that groups that mustered more aggressive participants were 14 times more likely to win an intergroup conflict than those with fewer (Chi-squared test: $\chi^2 = 26.900$, $df = 1$, $p < 0.001$). As a result, smaller groups were able to defeat larger groups during 41% of the intergroup conflicts they experienced.

Spatio-Temporal Variability in the Occurrence of Female-Male Aggression and Female-Male Grooming

We examined the spatio-temporal variability in the occurrence of FM-agg and FM-gr, and found that females were more likely to exhibit these behaviours in both the season when, and locations where high-quality food resources were available. Seasonal patterns of food availability were indexed using monthly NDVI values derived from satellite images of the study site, while the spatial distribution of food was calculated by mapping the distribution of important tree species throughout the study site, and monitoring the monthly availability of fruits on these tree species (see Chapter 4 Appendix). Social incentives were more commonly observed in the summer months (GLMM: $b \pm SE = 5.253 \pm 1.819$, $z = 2.888$, $p = 0.004$**;** Table A4.1), when tree species important in the diet of the monkeys were fruiting (Willems et al. 2009), and in areas of their home range that currently had the highest availability of fruits ($b \pm SE = 2.326 \pm 0.953$, $z = 2.441$, $p = 0.015$; Table A4.1). Thus, females were most likely to bestow social incentives in situations where and when valuable food resources were at stake.

Actors and Targets of Female-Male Aggression and Female-Male Grooming

Both putative punishment (FM-agg) and putative rewards (FM-gr) were rare events, with only 36 cases of the former and 35 cases of the latter observed throughout hundreds of intergroup encounters. Twenty-one

females were observed to exhibit FM-agg (10 in Group A, three in Group B, seven in Group C, and one in Group D), while seventeen different females were seen using FM-gr during intergroup encounters (six in Group A, four in Group B, six in Group C, and one in Group D). These actors ranged in rank from the dominant female to the lowest ranking female in their group. When putative punishment occurred during intergroup conflicts, and the actors were known, in 73% of cases it was the female(s) that had participated in the most recent act of intergroup aggression that exhibited FM-agg; alternatively, in 27% of cases FM-agg was exhibited by one or more bystanders. Similarly, putative rewards were typically bestowed soon after an aggressive episode (mean ± SD = 4.7 ± 4.6 min.) and the females that exhibited FM-gr were usually those who had participated in it (78% of cases). Although females sometimes acted alone, in 68% of cases FM-agg was exhibited by a coalition of females and/or juveniles (up to four individuals). Females who groomed male group members almost always did so alone.

We observed females directing putative punishment and rewards at a number of different males (FM-agg: five males in Group A, two in Group B, five in Group C, and at least one male in Group D; FM-gr: six males in Group A, three in Group B, five in Group C, and at least one male in Group D), and these targets could be either dominant or low-ranking males. When females utilised social incentives during intergroup conflicts, female actors were significantly more likely to use aggression when the target male had recently defected from participation, but use grooming with males who had recently participated (Fisher's exact test: $p < 0.001$; Figure 4.2a; Figure 4.3a). Males who were groomed by female group members had participated in the most recent act of intergroup aggression in 16 out of 23 (70%) of the observed cases (Figure 4.3a). Conversely, males who received FM-agg had not participated in the most recent aggressive episode in 20 out of 24 (83%) of the observed cases (Figure 4.2a). Furthermore, in two of the remaining 24 cases, the target male had recently participated but had begun to retreat from the front-line; thus, it is possible that females also perceived these retreating males as defecting. Notably, three males that were never observed to receive FM-gr were those that were rarely present near the front-line and were never observed to participate in intergroup conflicts in the absence of social incentives (Figure 4.1). Conversely, two males that were never observed receiving FM-agg were the two males in the population who were the most active in intergroup conflicts (participated in ~55% of aggressive episodes; Figure 4.1).

When the targets of female social behaviours are compared among contexts, we find that females were significantly more likely to target males, as opposed to females or juveniles, during intergroup conflicts than in other contexts. During intergroup conflicts, 36 out of the 41 observed cases (88%) of female aggression targeted males; conversely, in other contexts, females directed only 65 out of 360 observed acts of aggression (18%) towards male group members (Chi-squared test: $\chi^2 = 95.032$, $df = 1$, $p < 0.001$). During intergroup conflicts, 36 out of the 247 observed cases of female grooming (15%) targeted males; in other contexts,

females directed 202 out of 2284 grooming events (9%) towards males (χ^2 = 8.592, *df* = 1, *p* = 0.003). While the odds ratio indicates that females were twice as likely to direct grooming towards male group members during intergroup conflicts, female aggression was almost exclusively directed towards males (odds ratio = 33 times as likely to aggress males than females or juveniles).

Target Behaviour Following Female-Male Aggression and Female-Male Grooming

We analysed the effect that social incentives had on subsequent male participation, both at the population level and the individual level. At the population level, all observations of FM-agg (or FM-gr) were pooled and the identity of the target male was not considered. At this level, FM-agg had a strong impact on the subsequent behaviour of target males; the likelihood ratio indicates that targeted males were 11 times more likely to participate in the next aggressive episode following FM-agg (71% of cases, *n* = 17) than they were to have participated in the most recent episode before being targeted (Chi-squared test: χ^2 = 11.53, *df* = 1, *p* < 0.001; Figure 4.2a). Many males were only observed receiving FM-agg on one or two occasions and because there was not always an aggressive episode prior to, or following putative punishment, we were only able to perform the individual-level analysis on a subsample of seven of the nine males observed to receive FM-agg. Despite the low power associated with this limited sample size, we nevertheless detected a tendency for individual males to increase their participation following putative punishment (Wilcoxon signed ranks test: *w* = 2, *n* = 7 males, *p* = 0.093, *r* = 0.64; Figure 4.2b). The magnitude of the effect size in the individual analysis suggests that this statistical trend is biologically meaningful, as does the finding that targets of FM-agg subsequently participated above their base-line level (i.e. the proportion of episodes participated in when they had not been the male targeted by FM-agg; Wilcoxon signed ranks test: *w* = 27, *n* = 8 males, *p* = 0.035, *r* = 0.75; Figure 4.2c). The "future" aggressive episodes that punished males participated in could be relatively soon (i.e. within 1 min.) or up to an hour after they received FM-agg (mean ± SD = 14.6 ± 17.7 min.).

Because FM-gr largely targeted males who had participated in the most recent aggressive episode, the proportion of target males who participated in the next aggressive episode following putative rewards (13 out of 20 observed cases; 65%) was not significantly different from the proportion of target males who participated in the most recent episode (70%; Chi-squared test: χ^2 = 0.10, *df* = 1, *p* = 0.75; Figure 4.3a). Similarly, at the individual level, target males maintained a relatively high level of participation following FM-gr (Wilcoxon signed ranks test: *w* = 13.5, *n* = 11 males, *p* = 0.599, *r* = 0.16; Figure 4.3b). This propensity to participate following FM-gr was biologically significant, as the targets of putative rewards subsequently participated at levels significantly higher than their base-line level (Wilcoxon signed ranks test: *w* = 36, *n* = 10 males, *p* = 0.014, *r* = 0.77; Figure 4.3c). The future aggressive episodes in which groomed males participated

could occur relatively soon (i.e. within 2 min.) or up to 102 minutes after the reward was bestowed (mean ± SD = 23.8 ± 29.7 min.).

Discussion

The aim of this study was to determine if female vervet monkeys use the carrot (grooming) and/or the stick (aggression) to manipulate male participation in intergroup conflicts when the resources limiting to female fitness were at stake. We found that females were more likely to direct aggression towards males that had recently defected, but groom males that had recently participated in the intergroup conflict. Given that males that received either subsequently participated at levels above their personal base-line, both FM-gr and FM-agg indeed appear to function as social incentives that effectively promote male cooperation in this context. Importantly, we observed that smaller groups were able to win intergroup conflicts if they mobilised a greater number of aggressive participants, indicating there was a significant benefit to recruiting male group members. We also found that females were more likely to use social incentives when the benefits were greatest. That is to say, females used the carrot and the stick in both the season when, and areas of their home range where, valuable food resources were most abundant. Together, these findings suggest that successful recruitment using social incentives may be crucial to success in intergroup conflicts over fitness-limiting resources, and therefore have significant effects on the fecundity of females (Cheney and Seyfarth 1987; Lee and Hauser 1998; Robinson 1988; Takahata et al. 2006; Takahata et al. 1998; Williams et al. 2004).

Because of their larger body and canine size, males are likely the most valuable group members to recruit during intergroup conflicts. However, it is perhaps less clear why males should respond to such relatively low-cost incentives as FM-gr, or the risk of injury from FM-agg, with the relatively high-cost behaviour of participation in intergroup conflicts. Two possible explanations are that these low-cost incentives have consequences for male-female social relationships, and/or that receiving incentives influences the reputation of the target male with his group members (Henzi and Barrett 1999; Silk et al. 2006; Silk et al. 2010). Grooming and tolerance (i.e. the lack of aggression) are important services exchanged in the formation and maintenance of social bonds in primates (Henzi and Barrett 1999; Silk et al. 2006; Silk et al. 2010), and it is possible that punishment and rewards have a disproportionate impact on male behaviour because these social interactions influence the quality of male-female social relationships. That is to say, receiving punishment could damage the target male's social relationship(s), either with the female actor(s) directly (i.e. experience based) or with other female group members who observe the social incentive (i.e. reputation or information based). Conversely, receiving rewards could improve bond strength and potentially signal to other female group members that the target male is a valuable social partner. Thus, relatively low-cost incentives potentially carry higher-cost consequences in the long-term, and subsequently impact male fitness (e.g. male mating success).

Although both female aggression and grooming were significantly more likely to be directed towards males (versus females and juveniles) during intergroup encounters than in other contexts, our data do not allow us to discount the possibility that males were more frequently in close proximity during these encounters. However, while proximity could potentially influence the propensity to direct grooming towards male group members, increased proximity cannot explain the overwhelming extent to which females targeted males when being aggressive. In fact, female intragroup aggression was almost exclusively directed towards males during intergroup conflicts, which raises the question of why females would use punishment primarily on males, rather than also with other females and juveniles. As males are the largest age-sex class, recruiting males likely has a disproportionate effect on the group's fighting ability. Not only does their larger size give them a physical advantage, but their participation in intergroup aggression appears to decrease the perceived risk of injury for smaller females, as females are more likely to participate when they have more support from their male group members (Arseneau-Robar et al. 2017). Thus, recruiting males may also encourage more females to join in the fight and further increase the odds of winning. Moreover, there were also more opportunities to recruit defecting males as they frequently sat near the front-line without actively participating. Males who were investigating dispersal opportunities were often present near the front-line so that when the intergroup conflict died down, they could approach and attempt to affiliate with members of the opposing group. Males who were likely to have sired offspring also often sat near the front-line, monitoring the intergroup conflict, ready to respond defensively when potential offspring were perceived to be at risk (Arseneau et al. 2015). Conversely, females and juveniles who were not participating in the intergroup conflict typically avoided the front-line and were therefore not potential targets for punishment.

Although social incentives were typically observed during the pauses in intergroup conflicts, in some cases, they were bestowed when the groups were within visual range but were not interacting. Upon detecting another group nearby, it was often female group members who began to approach the opposing group while vocalising to solicit support. When "enough" group members had joined them (usually within 1 m), they initiated an escalated conflict. Thus, in gearing up for an intergroup conflict, it was often females who took the initiative, and who assessed if they had gathered sufficient willing participants, or whether they should retreat from a risky confrontation. In this context, FM-agg and FM-gr may function to goad males into supporting females in instigating intergroup conflicts. Further work is necessary to determine how the decision to escalate versus retreat is made, and the effect social incentives have on male behaviour in this context.

Both FM-agg and FM-gr were typically exhibited by females that had participated in the most recent aggressive episode (i.e. second parties); however, in a quarter of cases, social incentives were bestowed by female bystanders. Given the importance of food resources to female fitness (Lee and Hauser 1998; Robinson 1988; Takahata et al. 2006; Takahata et al. 1998; Williams et al. 2004), all female group members are likely to benefit

from forcefully recruiting male group members during intergroup conflicts. Thus, cases where punishment and rewards were bestowed by a bystander would most accurately be described as peer punishment and rewards (as opposed to social incentives provided by a centralised authority) exhibited by self-serving third parties (Baldassarri and Grossman 2011; Raihani et al. 2010; Raihani et al. 2012c). In primitive warfare, punishment and rewards are doled out both by other warriors (second parties) and other group members who are in many cases, likely to be self-interested third parties (Chagnon 1988; Glowacki and Wrangham 2013); however, there is also evidence that in larger groups, third parties who do not frequently interact with the target (i.e. individuals who do not gain significant direct benefits) also use social incentives to promote warrior participation (Mathew and Boyd 2011; Mathew and Boyd 2014). Communication can greatly enhance cooperation in social dilemmas (Balliet 2009; Deutsch 1958), as communication allows group members to gossip about the bravery, or cowardice of warriors. As a result, individuals may behave cooperatively to improve their reputation with their group members (Milinski et al. 2002) and social incentives are often bestowed by group members who were not present to observe the participation of warriors directly (e.g. women and senior group members) (Glowacki and Wrangham 2013; Mathew and Boyd 2011).

In this study, we were able to capitalise on the fact that intergroup conflicts in vervets consist of a number of episodes of intergroup aggression with pauses in-between. As a result, we have been able to assess if the targets of FM-agg and FM-gr had or had not participated in the most recent cooperative event, and if these social incentives promoted participation in future cooperative events. With these data, we demonstrate the first quantitative evidence that both positive and negative social incentives are used to effectively manipulate male participation in intergroup conflicts in a species other than our own. Furthermore, we have strived to describe the social and ecological conditions in which these social incentives occur, providing unique insight into the real-world conditions under which punishment and rewards can evolve. We urge other researchers who observe intragroup aggression and/or affiliative behaviours during (or shortly following) intergroup conflicts, as well as other cooperative activities, to also investigate who is the target of these behaviours, and the impact such social interactions have on future cooperative behaviour. Such investigations are critical to understanding how important social incentives are to the evolution and maintenance of cooperation in non-human animals.

Chapter 4 Figures

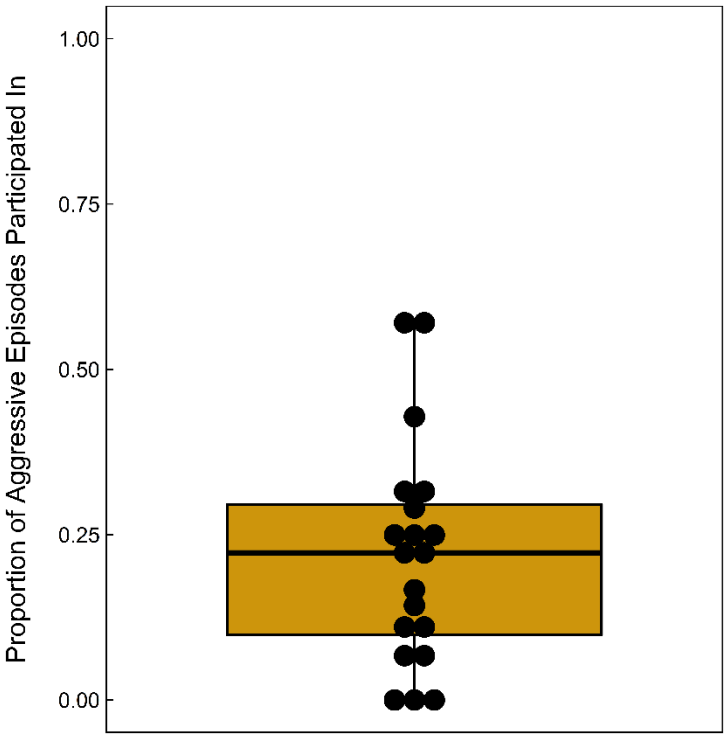

Figure 4.1 Typical levels of male participation in intergroup conflicts, calculated as the proportion of aggressive episodes that each male participated in during intergroup conflicts in which no social incentives (female-male aggression or female-male grooming) were observed. Each dot represents one male in the population (*n* = 20).

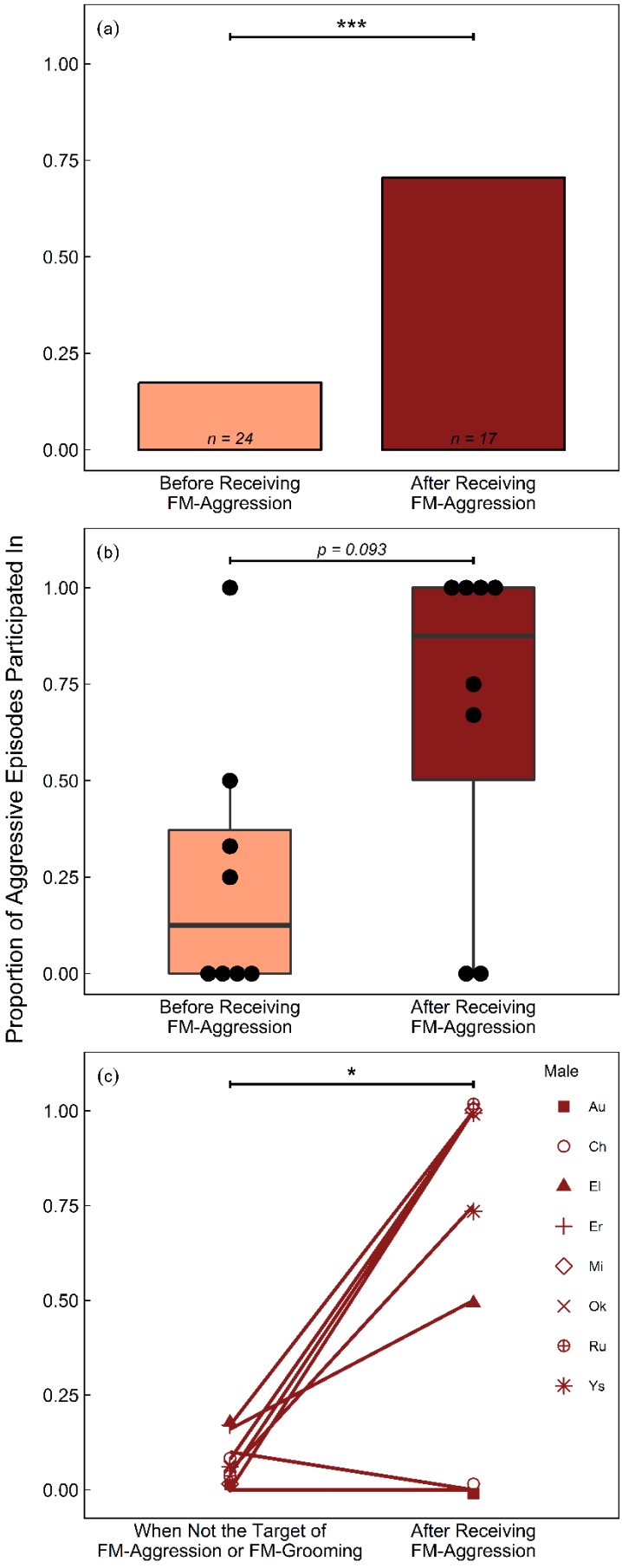

Figure 4.2 The proportion of aggressive episodes that targeted males participated in before (light) versus after (dark) receiving aggression from female group members (a) at the population level, and (b) at the individual level (note: each dot represents the proportion of aggressive episodes participated in for one male in the population (n = 9 males). (c) The proportion of aggressive episodes targeted males participated in after being aggressed by a female group member, compared to their base-line level of participation (i.e. proportion of episodes participated in during intergroup conflicts where social incentives were observed, but they were not the male targeted). Significance levels denoted by * ($p < 0.05$) and *** ($p < 0.001$).

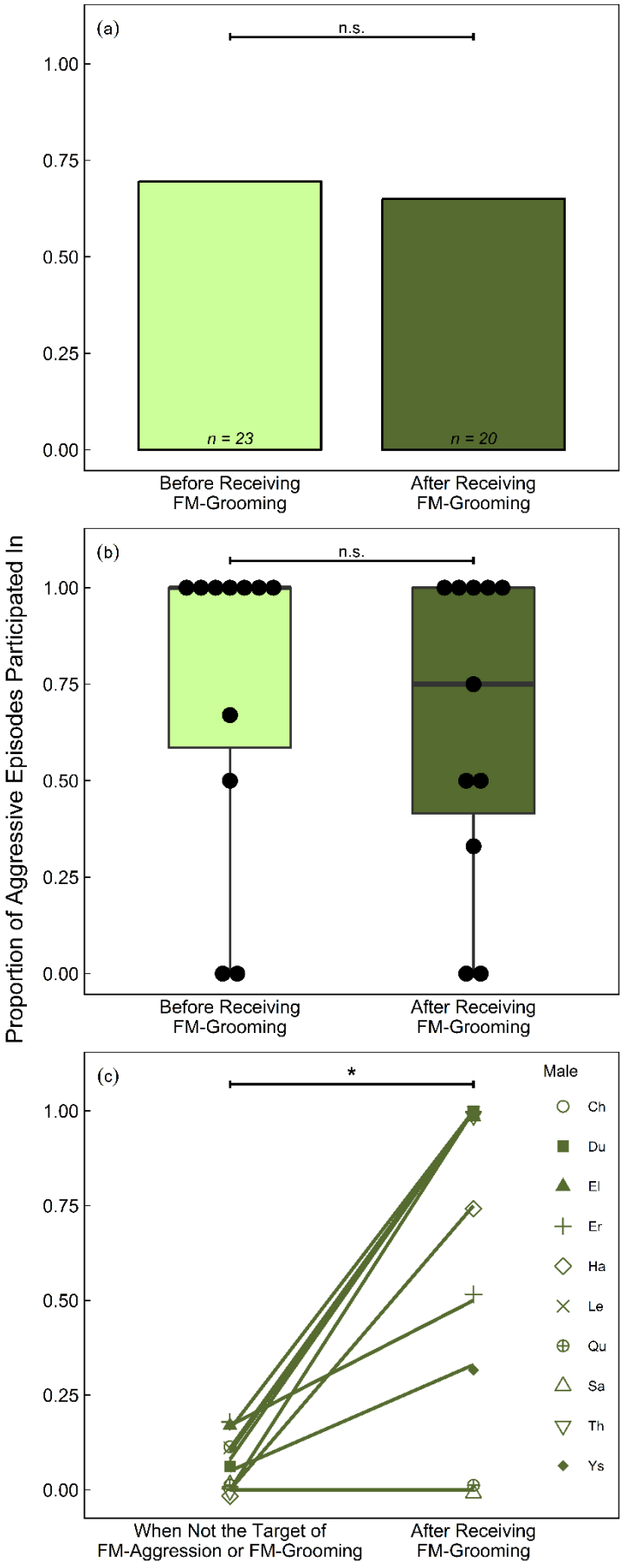

Figure 4.3 The proportion of aggressive episodes that targeted males participated in before (light) versus after (dark) receiving grooming from female group members (a) at the population level, and (b) at the individual level (note: each dot represents the proportion of aggressive episodes participated in for one male in the population (n = 11 males).

(c) The proportion of aggressive episodes targeted males participated in after being groomed by a female group member compared to their base-line level of participation (i.e. proportion of episodes participated in during intergroup conflicts where social incentives were observed, but they were not the male targeted). Significance levels denoted by * ($p < 0.05$) and *** ($p < 0.001$).

Chapter 4 Appendix

To understand if female-male aggression (FM-agg) and female-male grooming (FM-gr) function as social incentives which promote male participation in defending resources that limit female fitness, we investigate the spatio-temporal variability in the occurrence of these social behaviours. If females use aggression and grooming to manipulate males into fighting for food resources, females should be more likely to exhibit these behaviours during time periods (i.e. seasons), and in locations where valuable food resources are at stake.

To examine the impact food availability had on the propensity for females to use social incentives, we examined both the temporal and spatial distribution of fruits throughout the home range of each group of vervet monkeys. The temporal variability in food availability was indexed by the normalized difference vegetation index values (NDVI), which is a well-established proxy of the amount and vigour of green vegetation, and strongly correlates with field measurements of food availability and shelter in vervet monkeys (Willems et al. 2009). NDVI values were obtained from the MODIS MCD43A4 data set (version 5, processed by NASA's LP DAAC (NASA Land Processes Distributed Active Archive Center (LP https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mcd43a4) and redistributed by WAMIS at http:// wamis.meraka.org/za/). During the summer season, when NDVI values were high, a number of tree species important in the diet of vervet monkeys in this population produce fruits. Outside of the summer season when fewer fruits were available, the monkeys ate a more varied diet that included insects, tree sap and leaves.

In examining the spatial distribution of food, we determined the relative availability of fruits in the various areas of each group's home range, during each month of the study period. We first delineated each home range into different areas, or mapping units. Because the study site is comprised of a number of smaller farms, which had varying land uses but have been allowed to regenerate, as well as a number of natural (e.g. the river) and man-made (e.g. roads and fence-lines) linear features, the landscape is a mosaic of discrete areas. The vegetation varies greatly among mapping units and the boundaries between mapping units tend to be clear and identifiable by abrupt changes in the height, density and composition of the trees. The vervet monkeys also treated the landscape as being heterogeneous, as group members would spread out to forage, rest and socialize within a mapping unit, but group together and move as a cohesive group when travelling from one mapping unit to the next. Furthermore, when an intergroup conflict occurred, the winning group typically pursued the losing group to the boundary of the mapping unit to ensure that all of its members had left the contested area.

We then determined the relative calories available from fruits in each mapping unit, within each home range, each month of the study period. Throughout the study period we conducted monthly phenology sampling, where we estimated the number of fruits per tree on 10 trees of each of the nine species most commonly

consumed by the study subjects. We mapped the spatial distribution of these trees counting the number of each species in each cell of a 100 m by 100 m grid, which was overlayed over a map of the study area. We then determined the monthly caloric value of fruits in each grid cell using the four species that were most important in the diet of the study groups, but were also heterogeneously distributed such that their availability varied among mapping units; the calories per grid cell were calculated by multiplying the number of trees per cell by the average number of fruits per tree (from the phenology sampling), by the caloric value of each fruit (Barrett 2009; El Ayadi et al. 2012; Feedipedia 2015). The calories per grid cell were averaged within each mapping unit each month. Because the vervet monkeys engaged in intergroup conflicts throughout the year (i.e. in seasons of high and low food availability), we determined the relative (caloric) value of each mapping unit, each month, relative to what was available within the home range of each of the study groups. The relative value of each mapping unit (within each group's home range) was calculated by dividing the average calories available in each mapping unit, by the average calories available in the unit with the highest availability of calories that month.

We analysed the effect that the spatial and temporal distribution of food, as well as the impact that the birth season and mating season had on the occurrence of social incentives using a generalized linear mixed model (GLMM). The birth season was indexed by the number of small infants (less than three months old) in the group, and the dependent variable was whether or not either female-male aggression (FM-agg) or female-male grooming (FM-gr) were observed in a given intergroup encounter. We set group as a random effect, a binomial error structure and a logit link function. This analysis was only conducted on three of the four study groups as we only mapped the distribution of food resources for these three groups.

Social incentives were more commonly observed in the summer months (GLMM: $b \pm SE = 5.253 \pm 1.819$, $z = 2.888$, $p = 0.004$; Table A4.1), when NDVI values were high, and tree species important in the diet of the monkeys were fruiting (Willems et al. 2009). Females were also more likely to exhibit FM-agg and FM-gr when the intergroup conflict took place in an area of their home range that currently had a relatively high availability of fruits ($b \pm SE = 2.326 \pm 0.953$, $z = 2.441$, $p = 0.015$; Table A4.1). Thus, females appear most likely to bestow social incentives in situations where valuable food resources were at stake. Conversely, the birth season ($b \pm SE = -0.112 \pm 0.095$, $z = -1.182$, $p = 0.237$; Table A4.1) and the mating season ($b \pm SE = 0.442 \pm 0.512$, $z = 0.864$, $p = 0.387$; Table A4.1) had no effect on the propensity for females to exhibit FM-agg and FM-gr.

Table A4.1 Spatio-temporal variability in the occurrence of social incentives (female-male aggression and grooming) during intergroup conflicts in vervet monkeys. The birth season was indexed by the number of small infants (less than three months old) in the group and the summer season was indexed using monthly normalized difference vegetation index values (NDVI), which correlate with field measurements of food availability in vervet monkeys. Relative food availability was determined by mapping the distribution and monthly phenology of tree species important in the diet of vervet monkeys at this field site, and comparing the relative availability of fruits in different areas of each group's home range.

Fixed Effects	***b* Estimate**	**SE**	***z***	***p***
Intercept	-6.033	1.333		
Birth season	-0.112	0.095	-1.182	0.237
Summer season	**5.253**	**1.819**	**2.888**	**0.004**
Mating season	0.442	0.512	0.864	0.387
Relative food availability	**2.326**	**0.953**	**2.441**	**0.015**

The model performed significantly better than the null model which contained only an intercept and group as a random effect (likelihood ratio test: $n = 274$, $\chi^2 = 77.15$, $p < 0.001$, $R^2_{GLMM(c)} = 0.21$). Significant predictors are presented in bold.

CHAPTER 5

Male monkeys use punishment and coercion to de-escalate costly intergroup conflicts

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Redouan Bshary and Erik P. Willems

In numerous social species, males direct aggression towards female group members during intergroup conflicts, and this behaviour is commonly thought to function as mate guarding, even though males often target non-receptive females. In studying intergroup conflicts in a wild population of vervet monkeys, we found that male intragroup aggression was primarily directed towards individuals who had either just finished exhibiting, or were currently attempting to instigate intergroup aggression. Targeted females were less likely to instigate intergroup aggression in the future, indicating that male intragroup aggression functioned as coercion (when directed towards those who were currently trying to instigate a conflict) and punishment (when directed towards those who had recently fought). These manipulative tactics effectively prevented intergroup encounters from escalating into conflicts. Males who were likely sires were those most likely to use punishment/coercion, particularly when they were wounded, and therefore less able to protect vulnerable offspring should a risky intergroup conflict erupt. This work, along with our previous finding that females use punishment and rewards to recruit males into fighting in intergroup conflicts, highlights the inherent conflict of interest that exists between the sexes, as well as the role that social incentives can play in resolving this conflict.

Introduction

Social groups are typically a heterogeneous assemblage of individuals, who each obtain different benefits, and experience different costs, from living and interacting with their fellow group members. As a result, conflicts of interest can arise between group members, including between siblings, parents and offspring, dominants and subordinates, or males and females (Huntingford and Turner 1987). Ultimately, the conflict of interest between the sexes stems from the asymmetry in their reproductive investment, with females typically investing more in each reproductive event. As a result, female fitness is typically limited by the resources required to produce and raise offspring, whereas male fitness is primarily limited by access to receptive females (Trivers 1972). Therefore, males and females tend to have different intrinsic interests, experience different selective pressures, and evolve different fitness-maximizing strategies (Fashing 2001; Muller and Wrangham 2009; Smuts and Smuts 1993; Trivers 1972). For example, male mating strategies may aim to maximise mate quantity while female mating strategies focus more on mate quality (Muller and Wrangham 2009; Smuts and Smuts 1993).

Because of their different intrinsic interests, and the importance of defending access to fitness-limiting resources, in social species, males and females are expected to have different strategies for participating in intergroup conflicts. Findings from a number of studies support this supposition, as females typically fight to obtain resources such as territory, food, water and shelter (Boydston et al. 2001; Nunn and Deaner 2004; Zhao and Tan 2010), while males tend to fight to defend mates (Kitchen et al. 2004; Koch et al. 2016; Majolo et al.

2005), or when they are able to assess paternity, to protect their offspring (Arseneau et al. 2015; Grinnell et al. 1995; Wich et al. 2004). Regardless of an individual's motivation for fighting, winning an intergroup conflict usually results in the defence of the contested area and the resources therein (e.g. food, water or shelter), at least in the short-term. Because all group members have access to these resources, cooperative intergroup aggression often produces a public good (Olson 1965). For some group members, however, the costs associated with participating in, or even experiencing an intergroup conflict, may outweigh the potential benefits associated with winning, or having access to the public goods produced. The risk of injury or death is a significant cost associated with intergroup conflicts (Cant et al. 2002; Cheney and Seyfarth 1987; Hölldobler and Lumsden 1980; Mech 1994; Mosser and Packer 2009). When sexual dimorphism is high, the risk of injury can prohibit members of the smaller sex from fighting (Cheney 1987; Koch et al. 2016; Willems et al. 2013); however, the most vulnerable group members are often infants (Arseneau et al. 2015; Borries 1997; Cheney and Seyfarth 1987; Cords and Fuller 2010; Harris and Monfort 2003; Mohnot 1980; Shopland 1982; Steenbeek 1999; Watts 1989; Watts et al. 2006; Wilson and Wrangham 2003). Thus, individual group members may vary in the level of risk they perceive intergroup conflicts to pose, depending on their sex and reproductive status. When the level of risk outweighs the potential benefits, individuals may prefer to avoid escalated intergroup conflicts, such that different group members may disagree on when to fight versus when to flee. These conflicts of interests impede effective group-level cooperation, and natural selection could favour the evolution of manipulative tactics that effectively influence the behaviour group members.

Both theoretical models of n-player cooperation (i.e. cooperation in a group setting) and public goods experiments on humans in the lab often conclude that social incentives such as rewards, punishment, or reputation effects, can effectively influence the behaviour of group members (Balliet et al. 2011; Fehr and Gächter 2000; Hardin 1968; Milinski et al. 2002; Nunn and Lewis 2001; Olson 1965; Sefton et al. 2007). Thus, in theory, social incentives could be used to resolve conflicts of interest that arise between group members in the context of intergroup conflicts. Although there is evidence that non-human animals use social incentives in dyadic cooperation (Bshary and Grutter 2005; Raihani et al. 2010; Raihani et al. 2012a; Raihani et al. 2012b), we know relatively little about the role that social incentives play in the production of public goods (Bshary and Bshary 2010). However, it was recently demonstrated that social incentives, including the punishment of defectors and rewarding of co-operators, are used by female vervet monkeys (*Chlorocebus aethiops pygerythrus*), to influence the participation of male group members during intergroup conflicts (Arseneau-Robar et al. 2016b).

Vervet monkeys live in multi-male multi-female groups, and although males are approximately 1.5 times larger than females, dimorphism is moderate enough that both sexes participate aggressively during intergroup conflicts (Arseneau-Robar et al. 2017; Arseneau et al. 2015; Cheney 1981). However, conflicts of interest may

arise between the sexes as females and males each appear to gain different benefits, and face different costs, from participating in, or even experiencing escalated intergroup conflicts. Although females appear sensitive to the risk of injury associated with fighting against larger-bodied males, they often instigate intergroup aggression, particularly when defending access to high-quality food resources (Arseneau-Robar et al. 2017). Conversely, males are less likely to defend food resources (Arseneau-Robar et al. 2016a; Arseneau et al. 2015), although they may support females in doing so if it is the mating season and they can enjoy greater mating success as a result (Arseneau et al. 2015). If male support is lacking and high-quality food resources are at stake, females use both punishment (i.e. intragroup aggression) and rewards (i.e. intragroup grooming) to recruit support from their male group members (Arseneau-Robar et al. 2016b). Because groups that mount a larger number of aggressive participants are more likely to win intergroup conflicts, recruiting males may increase the odds that females successfully gain access to contested resources (Arseneau-Robar et al. 2016b).

Male vervet monkeys in the same population have also been observed to both aggress and groom their fellow group members during intergroup conflicts; however, it is still unclear if male intragroup aggression (hereafter 'male aggression') and male intragroup grooming (hereafter 'male grooming") also function as social incentives. In vervet monkeys, infants who are less than a year old are those most likely to suffer fatal injuries during intergroup conflicts (Arseneau et al. 2015; Cheney and Seyfarth 1987). Both mothers, and males who are likely to have sired infants, appear to be sensitive to this risk (Arseneau-Robar et al. 2017; Arseneau et al. 2015). However, because food resources are an important factor limiting female fitness, females with infants benefit if their group wins intergroup conflicts. It appear that females with infants mitigate the risks posed to infants by avoiding the front-line of intergroup conflicts, leaving the fighting to other group members (Arseneau-Robar et al. 2017). Males who are likely to have sired infants appear to employ a different strategy. Likely sires tend to sit vigilant at the front-line ready to respond defensively if the opposing group's members are highly aggressive; thus, they appear to be reactive and protective rather than keen to instigate intergroup encounters into intergroup conflicts (Arseneau et al. 2015). Given the risks that escalated intergroup conflicts pose to offspring, and that male fitness is less likely to be dependent on winning access to food resources, males who are likely sires may benefit from preventing intergroup encounters from erupting into intergroup conflicts, or to de-escalate ongoing conflicts. A second reason that males may want to de-escalate intergroup conflicts is that the calm periods, when the two groups are near to each other but not fighting, give males the chance to mingle and affiliate with members of the opposing group (Arseneau et al. 2015; Teichroeb et al. 2011). Thus, non-escalated intergroup encounters provide a valuable opportunity to assess dispersal opportunities (i.e. to prospect) (Arseneau et al. 2015; Teichroeb et al. 2011).

Conflicts of interest could also arise between the sexes if females engage in extra-group copulations. If male aggression and/or grooming decrease the likelihood that females fraternize with extra-group males, these

behaviours could serve a mate defence function (Cheney 1987; Cheney and Seyfarth 1977; Feist and McCullough 1976; Kummer 1968; Sicotte 1993). The primary goal of this study was to determine if male intragroup aggression and/or grooming function as mate defence, or to de-escalate intergroup conflicts. If either of these behaviours function as mate defence, they should be exhibited during the mating season when females could be receptive, and only be directed towards female group members. Male aggression should target females who are affiliating or mating with extra-group males, and grooming should be bestowed on females who avoid extra-group males. Conversely, if males are trying to de-escalate intergroup conflicts, then they may be more likely to exhibit intragroup aggression and/or grooming during the summer season as this is the time of year when females are most likely to instigate and fight in intergroup conflicts (i.e. is when conflicts of interest are likely to arise), as well as when intergroup conflicts were of a long duration and therefore offered the greatest prospecting opportunities (Arseneau-Robar et al. 2017; Arseneau et al. 2015). Male aggression should be directed towards group members who are trying to instigate intergroup aggression (i.e. to coerce them into behaving less aggressively), or individuals who have recently exhibited intergroup aggression (i.e. as a punishment for fighting). Male grooming should be directed towards individuals who do not participate aggressively in the intergroup conflict. Moreover, these behaviours should decrease the likelihood that the target participates aggressively in the intergroup conflict in the future, and may even de-escalate the entire intergroup conflict. If males de-escalate intergroup conflicts to increase prospecting opportunities, male aggression and/or grooming should be exhibited by males who are attempting to affiliate with the members of the opposing group during the intergroup encounter. If males de-escalate intergroup conflicts to protect offspring, male aggression and/or grooming should be exhibited by males who are likely to have sired offspring, that is to say, males who were resident in the group the previous mating season and had a high proportion of the observed matings. Furthermore, likely sires may be particularly averse to the risks posed to offspring if they themselves are wounded, and therefore less able to effectively defend vulnerable infants, should the need arise. The second goal of this study was to compare the male intragroup aggression and grooming to the observed patterns of punishment and rewards observed in females, to better understand how the conflict of interest arises in this species, and how it is resolved. Thus, we examine the temporal co-occurrence of intragroup aggression and grooming in males and females.

Methods

Subjects and Study Site

Data were collected on four groups of vervet monkeys at the Mawana Game Reserve (28°00'S, 31°12'E), South Africa, between January 2012 and February 2014. All animals were individually recognized and each group contained one to seven adult males and five to 14 adult females. The adult members of the frequently encountered neighbouring groups were also recognized, but we did not collect detailed behavioural data on

these groups. All data collection protocols were approved by the appropriate local authority, the Ezemvelo KZN Wildlife Board.

Behavioural Data

More than 11000 hours of behavioural data were collected, with researchers spending one to two full days with each group, each week. On each observation day, researchers recorded if any group members have visible wounds or injuries, conducted group scans every 30 minutes, and also recorded all occurrences of social interactions (e.g. aggression, grooming and matings). We calculated the proportion of matings that each male obtained in a given mating season, and classified males as likely sires if they had obtained greater than 20% of the matings in their group the previous mating season (Arseneau et al. 2015). Each group contained one to three likely sires and up to five males with a low probability of having sired offspring (Arseneau et al. 2015). We classified males as being wounded if a visible wound had appeared within the last two weeks, as this was the average amount of time it took for wounds to heal.

Information on individual participation during intergroup encounters was collected on an all-occurrence basis, with observers noting the time of all participation events, the participants, and their behaviour (Altmann 1974). Participation could be non-aggressive (e.g. being vigilant, making intense contact calls, or approaching closer), aggressive (e.g. running towards the opposing group while making aggressive vocalizations or chasing individuals), or affiliative (e.g. sitting in close proximity, playing or grooming). Males who attempted to affiliate with members of the opposing group were classified as prospecting for that intergroup encounter. Non-aggressive behaviours functioned to alert group members to the presence of the opposing group, but also to solicit support before initiating an act of intergroup aggression (hereafter, an 'aggressive episode'). For example, individuals attempting to instigate intergroup aggression typically began to approach the opposing group while making intense contact calls (hereafter, an 'instigating episode'). Group members willing to provide support joined them and often also contact called such that their vocalizations were done in a loud chorus. The instigator and supporter(s) then exhibited cooperative intergroup aggression (Arseneau-Robar et al. 2016b). Thus, approaching and making intense contact calls were the behaviours typical of an individual attempting to instigate intergroup aggression and escalate an intergroup encounter into an intergroup conflict. We used this dataset to determine if the targets of male intragroup aggression and grooming were affiliating with an extra-group males, attempting to instigate intergroup aggression, or had participated in the most recent aggressive episode. We also determined if the target(s) subsequently attempted to instigate intergroup aggression or participated in the next aggressive episode.

Statistical Analyses

We examined the temporal variability in the occurrence of male aggression and grooming using two generalized linear mixed models (GLMMs), in which the dependent variable was whether or not male aggression, or male grooming, were observed in each intergroup encounter. We included the group as a random effect, set a binomial error structure and a logit link function, and tested three seasonal fixed effects. The three seasons important in this population are the birth season, the summer season when high-quality food resources are available, and the mating season (Arseneau-Robar et al. 2016b; Arseneau-Robar et al. 2017; Arseneau et al. 2015). The birth season was indexed by the number of small infants (less than three months old) in the group, and the summer season was indexed using monthly average normalized difference vegetation index values (NDVI). NDVI values correlate with field measurements of food availability and shelter in vervet monkeys (Willems et al. 2009), and were obtained from the MODIS MCD43A4 data set (version 5, processed by NASA's LP DAAC (NASA Land Processes Distributed Active Archive Center)) (https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mcd43a4) and redistributed by WAMIS at http:// wamis.meraka.org/za/).

We used a Wilcoxon signed ranks test to examine the impact that male intragroup aggression had on the behaviour of target females (i.e. before versus after being targeted). For each female who was targeted, we determine the proportion of cases in which they had either been attempting to instigate intergroup aggression, or had participated in the most recent aggressive episode; similarly, we calculated the proportion of cases each female participated in either an instigating episode, or an aggressive episode following male aggression. We examined the biological relevance of the observed effect by comparing the likelihood that targeted females participated aggressively following male aggression to their base-line likelihood of participating in two consecutive aggressive/instigating episodes. This likelihood was determined for each female using their observed participation in intergroup conflicts in which no social incentives were observed. Female participation following male aggression was compared to their base-line expectation using a Wilcoxon signed ranks test.

A Fisher's exact test was used to compare the likelihood that an intergroup encounter escalated into an intergroup conflict, if males did versus did not exhibit intragroup aggression when the two groups were nearby, but not yet fighting. Because male grooming was observed very rarely, we were unable to conduct a formal statistical test on the behaviour of targets before versus after grooming. Therefore, we present only summary statistics and anecdotal evidence in discussing the function of male grooming.

We used a GLMM to test the impact that male characteristics had on their propensity to exhibit intragroup aggression during intergroup conflicts. The dependent variable was whether an individual male exhibited intragroup aggression in a given intergroup encounter. The fixed effect, male characteristics, classified males

as, (1) wounded likely sires, (2) healthy likely sires, (3) males who were wounded but not likely to have sired offspring, (4) males who were using the intergroup conflict to prospect, and (5) and the reference category, males who were not wounded, prospecting or a likely sire. We included individual nested within group as a random effect. A GLMM was also used to investigate the seasonal co-occurrence of male and female social incentives, testing whether the sexes tended to both use intragroup aggression and grooming during the same months. The dependent variable was whether male intragroup aggression was observed in a given group in a given month. The fixed effect was whether female social incentives (either punishment or rewards) were observed in that same group and month, and group was included as a random effect. In all analyses, α was set at 0.05, but we also discuss non-significant trends ($0.05 < p < 0.10$) when they are biologically interesting. The overall significance of each GLMM was assessed by comparing the final model to the null model (model including intercept and random effects only) using a likelihood ratio test. All statistical analyses were conducted in R (version 3.0.3, R Core Team 2014) and we used the lme4 package (version 1.1-4, Bates et al. 2015) to fit the GLMM models.

Results

We observed more than 400 intergroup encounters and approximately half of these (*n* = 236) escalated into intergroup conflicts, which could last for up to 8 hours (mean ± SD = 45 ± 55 min., range = 1 to 475 min.). Male intragroup aggression during intergroup encounters was only observed 37 times during the two-year study period; male intragroup grooming was even more rare, with only 12 cases observed during the study period. Male aggression was more likely to occur in the summer season than at other times of year, but we detected no seasonal variability in the occurrence of male grooming (Table 5.1).

Male Intragroup Aggression

Males exhibited aggression when the opposing group was nearby but no fights had yet broken out (*n* = 17), as well as during escalated conflicts (*n* = 20). Although male aggression sometimes took the form of a chase (*n* = 11), in many cases, the male only used a threatening display such as a stare attack (*n* = 26); neither chases nor displays caused the target and/or the rest of the group to move away from the opposing group. We observed only two cases where males directed aggression towards females who behaved affiliatively (i.e. sitting in close proximity or grooming) towards extra-group males **(**Figure 5.1). This observation, combined with the lack of a mating season effect (Table 5.1), suggests that while male aggression may function as mate defence in rare cases, this explanation does not appear to explain most of male aggression observed in this species.

Male aggression was usually directed towards one or more adult females (*n* = 18), or females and juveniles (*n* = 12), but in 19% of cases (*n* = 7) males targeted solely juveniles; in four of these cases the targeted juvenile

was a male, and was therefore, not a potential future mate. Sixteen individual adult females were observed to receive male aggression. In the majority of cases, the target(s) were behaving aggressively towards the members of the opposing group (76%) rather than affiliatively (5%) (Figure 5.1). More specifically, the targeted individual(s) had just finished an act of intergroup aggression in 11 cases, or were currently instigating an aggressive episode (i.e. by vocalizing while being vigilant towards and/or approaching the opposing group) in 17 cases. In seven cases, although the target was at the front-line and vigilant, it could not be determined if they were attempting to escalate the intergroup conflict.

We assessed if male aggression discouraged the target(s) from participating in instigating episodes or aggressive episodes in the future. To do this, we compared the proportion of cases in which each female had either participated in the last aggressive episode or was currently trying to instigate intergroup aggression, to the proportion of cases in which she participated in the next aggressive or instigating episode. We find that male aggression had a strong effect on the subsequent behaviour of females, as female targets were significantly less likely to attempt to instigate aggression, or participate in the next aggressive episode to occur after they were attacked (Wilcoxon signed ranks test: $w = 105$, $n = 16$ females, $p < 0.001$, $r = -0.83$; Figure 5.2a). Thus, male intragroup aggression appeared to coerce individuals who were currently trying to instigate intergroup aggression into decreasing their activity level, and to function as punishment, when directed towards individuals who had just finished fighting in the intergroup conflict. Because females whose behaviour before being attacked was unconfirmed, were scored as not being aggressive or escalating intergroup aggression, the estimated propensity for target females to decrease their level of activity after being attacked is conservative.

Individual participation in intergroup conflicts in vervet monkeys is highly variable. Therefore, the observed decrease in female activity following male aggression could also arise if females typically only participate in a single aggressive episode before retreating from the front-line. To ensure that the observed propensity for targeted females to reduce their level of activity is indeed biologically meaningful, we determined each female's base-line likelihood of participating in two consecutive aggressive/instigating episodes. We find that females who instigate or engage in intergroup aggression often also participate in the next instigating/aggressive episode (Figure 5.2b). Thus, the observed effect that male coercion/punishment had on the behaviour of female group members appears biologically meaningful, as targeted females would be expected to continue to participate in subsequent instigating/aggressive episodes had they not been attacked (Wilcoxon signed ranks test: $w = 7$, $n = 15$ females, $p = 0.003$, $r = -0.77$; Figure 5.2b). When coercion was used prior to the onset of any intergroup aggression (i.e. the two groups were near each other, but not yet fighting), the intergroup encounter was less likely to escalate than if no coercion had occurred (Fisher's exact test: $p = 0.005$). Furthermore, in the three cases where an intergroup conflict eventually erupted, this escalation did

not occur for over an hour (range: 67 to 73 min.). When male aggression was used during an escalated intergroup conflict, the conflict subsequently ended with no further acts of intergroup aggression in 9 out of 20 cases.

Of the 15 individual males who exhibited intragroup aggression during intergroup conflicts (6 in group A, 5 in group B, 3 in group C, and 1 in group D), 12 were adult males and three were subadult males, who had not yet emigrated from their natal group. Among adult males, those most likely to use coercion/punishment were males who had achieved high mating success the previous mating season, and so were likely to have sired offspring in their group, particularly if they were wounded **(**Table 5.2). Of the 32 cases where coercion/punishment was exhibited by an adult male, he was a likely sire in 24 cases; although we lacked mating data to evaluate their probability of paternity, the actor may have been a likely sire in an additional 3 cases, as they had been resident in either their current group or the opposing group the previous mating season. The effect of being wounded appears to be additive to being a likely sire because males who were wounded, but were not likely sires, were no more likely to exhibited coercion/punishment than males in the reference category (males who were not wounded, likely sires, or prospecting) (Table 5.2). In fact, males who were wounded when they exhibited male aggression were always likely sires, or in one case, potentially a sire in the opposing group. Interestingly, all of the observed cases of coercion/punishment by a wounded male occurred during the mating season. Therefore, although we did not detect a significant mating season effect in the occurrence of male aggression (Table 5.1), any apparent mating season effect likely arises because of the increased rates of wounding during this period.

Although males who were prospecting were not significantly more likely to exhibit male aggression than males in the reference category (Table 5.2), some cases of male aggression may have served this function as we found a non-significant trend. However, using coercion/punishment to de-escalate intergroup conflicts may be an important strategy for subadult males in this population. In all cases where the actor was a subadult male (*n* = 5), they exhibited male aggression during intergroup encounters in which they were attempting to affiliate with members of the neighbouring group. They had also been observed prospecting during other intergroup encounters over the past month, indicating that they were likely actively assessing dispersal opportunities.

Male Intragroup Grooming

Only three males (1 in Group A, and 2 in Group B) were observed grooming fellow group members during intergroup conflicts, and the majority of cases were from a single individual (*n* = 9 out of 12 cases). There was no clear pattern in the identity of the individuals exhibiting male grooming, with 7 cases being exhibited by an actor who was a likely sire and 5 by a male who had either not been present the previous mating season, or

had had very low mating success. Grooming was never exhibited by a male who was wounded or prospecting. There was also no clear pattern in the behaviour of individuals targeted either before or after being groomed. In the 10 cases where the behaviour of the targets was known, they had recently engaged in or were currently trying to instigate intergroup aggression in six cases; in three cases, the targeted female participated in instigating or aggressive episodes after being groomed.

Comparing Male and Female Social Incentives

Just as female social incentives were more likely to be used in the summer season when fruits were most abundant (Arseneau-Robar et al. 2016b), males were also more likely to exhibit punishment/coercion in the summer season (Table 5.1). As a result, there was a significant positive relationship in the monthly occurrence of male and female social incentives (GLMM: $b \pm SE = 1.680 \pm 0.631$, $z = 2.662$, $p = 0.008$), and in some cases, these incentives were exchanged within the same intergroup encounter. Of the 26 separate intergroup encounters in which male aggression was observed, females also employed social incentives in 8 (~30%). In such encounters, the social incentives were usually exchanged between different actors and targets, rather than between the same pairs of individuals.

Discussion

The goal of this study was to investigate the function of male intragroup aggression and grooming during intergroup encounters in vervet monkeys. Our findings support that male intragroup aggression coerced individuals who were currently trying to escalate the intergroup encounter into decreasing their level of activity; when directed towards individuals who had just finished exhibiting intergroup aggression, male aggression functioned as punishment, effectively decreasing the likelihood that targeted individuals instigated or participated in intergroup aggression in the future. This observed decrease is biologically meaningful, as females were less likely to participate after being coerced/punished than would be expected, given their base-line levels. In many cases these manipulative tactics de-escalated the entire intergroup encounter.

Males who were likely sires were those most likely to use punishment and coercion, particularly when they were wounded, suggesting that likely sires try to de-escalate the situation when an escalated conflict would pose a risk to offspring. The wounds that males suffered could be severe, and included having their upper lip bitten off, gashes across their torso, and bites that removed chunks from their tail or buttocks. Thus, wounded males may have felt unable to fight defensively, or to retrieve an infant should the need arise. Given that we observed infants less than a year old being attacked on three occasions and one of these resulted in death (Arseneau et al. 2015), the risk of infant attacks are very real in this population. Males, and subadult males in particular, may use manipulative tactics when an escalated intergroup conflict would disrupt a valuable

prospecting opportunity. In addition to providing males the chance to assess the composition (i.e. number of potential mates and number of potential rival males) of the neighbouring group, calm periods during intergroup encounters also allowed males to mingle and try to affiliate with the members of the opposing group. The extent to which females tolerate prospectors, or even affiliate with them, and the amount of aggression prospectors receive from males in the opposing group, likely allow prospecting males to gauge how easily they might integrate into the group if they did disperse (Teichroeb et al. 2011). Furthermore, prospecting during intergroup encounters may be less risky than prospecting alone because if attacked, males, subadults in particular, often receive support from their group members.

These findings are in opposition to the long-held assumption that males use intragroup aggression to herd females away from extra-group males during intergroup conflicts, and therefore that this behaviour functions as mate defence (Cheney 1987; Klingel 1969; Kummer 1968; Monard et al. 1996). The punishment/coercion function may be widespread (See Chapter 5 Appendix); whenever one or more group members are motivated to fight, but the intergroup conflict is perceived as costly to males, they have an incentive to manipulate the behaviour of their fellow group members. Males in a number of species may perceive escalated intergroup conflicts as costly because of the risk of infant attacks during intergroup conflicts (Arseneau et al. 2015; Borries 1997; Cheney and Seyfarth 1987; Cords and Fuller 2010; Harris and Monfort 2003; Mohnot 1980; Shopland 1982; Steenbeek 1999; Watts 1989; Watts et al. 2006; Wilson and Wrangham 2003), or because they use intergroup encounters to assess dispersal opportunities (Cheney 1981; Cheney and Seyfarth 1977; Doolan and Macdonald 1996; Lazaro-Perea 2001; Majolo et al. 2005; Marty et al. 2016; Teichroeb et al. 2011; van Noordwijk and van Schaik 2001). To determine if male aggression functions as mate defence or to manipulate the aggressive participation of the targeted group member, it is critical that future studies document the behaviour of the targeted individual(s), both before and after receiving male aggression.

We did not find any strong evidence that male intragroup grooming functioned to manipulate the behaviour of group members. When aggressive conflicts arise within social groups, the participants can engage in post-conflict affiliation, either with the individual they had the conflict with, or other group members. Such post-conflict affiliation may decrease stress levels by decreasing the heart rates of the affiliating individuals, reconcile relationships, or console and calm the targets of aggression (Aureli et al. 1999; Aureli and Schaik 1991; Cheney and Seyfarth 1989; de Waal and van Roosmalen 1979). Fighting in intergroup conflict is likely just as, if not more, stressful than engaging in intragroup conflict, and so grooming could be used to relieve stress. In contrast to this finding, our previous work demonstrated that females use grooming to reward males who have recently participated in the intergroup conflict, and targeted males maintain their high level of participation in the future (Arseneau-Robar et al. 2016b). If social incentives evolved by hijacking a pre-existing stress response, the lack of a male reward system may arise because the necessary associations are difficult

to learn (Raihani et al. 2012c). In the female reward system, females groom males who have recently participated in the intergroup conflict; as such, grooming takes place shortly following an act of intergroup aggression. Conversely, if a male reward system did evolve, we would expect males to groom (i.e. reward) females who did not instigate intergroup aggression. Thus, grooming would have to be initiated when the intergroup encounter was calm, and females would have to learn to associate male grooming with their doing nothing. This association is likely more difficult to make than to learn that grooming is linked to active participation in the intergroup conflict.

Because male and female vervet monkeys experience very different costs and benefits from fighting in intergroup conflicts (Arseneau-Robar et al. 2016a; Arseneau-Robar et al. 2017; Arseneau et al. 2015), they likely disagree on when to fight versus when to avoid engaging in intergroup aggression. This conflict of interest has severe consequences for group-level cooperation in this context. Females use both positive and negative social incentives to recruit males to fight in intergroup conflicts, thereby promoting more effective group-level cooperation (Arseneau-Robar et al. 2016b). Conversely, males attempt to inhibit females from escalating intergroup encounters into high-risk conflicts, subsequently stifling group-level cooperation. These social incentives are primarily exchanged during the summer season, when females have much to gain from winning access to high-quality food resources, and are therefore, more likely to instigate intergroup conflicts that males perceive as costly (Arseneau-Robar et al. 2016b; Arseneau-Robar et al. 2017). In addition to being used in the same season, social incentives can be exchanged between males and females within the same intergroup conflict. It therefore appears that in vervet monkeys, punishment, coercion and rewards are all used to negotiate cooperative intergroup aggression with members of the opposite sex. This finding is in contrast to other studies showing non-human animals using only negative social incentives (Clutton-Brock and Parker 1995; Raihani et al. 2012c). For example, studies that have demonstrated that punishment is used to promote cooperation between two partners (i.e. dyadic cooperation) have found that only the larger partner punishes the smaller partner (i.e. punishment is asymmetric) (Bshary and Grutter 2005; Raihani et al. 2010; Raihani et al. 2012a; Raihani et al. 2012b). Because of the risk of retaliation by the target represents an additional cost to punishing, punishment is thought to be more likely to evolve when there are power asymmetries between individuals (Clutton-Brock and Parker 1995; Raihani et al. 2012c). Given their larger size, it is not that surprising that male vervet monkeys are able to punish females. However, females face a significant risk of injury if a male retaliates when punished, and females often use coalitions to mitigate this risk and tip the balance of power in their favour (Arseneau-Robar et al. 2016b). Because coalitions cannot be used to undermine the power held by larger, stronger, or higher-ranking individuals when cooperation takes place in a dyadic setting, it is not possible to create an asymmetry in numbers. As a result, the negotiation process observed in the vervet monkeys, with both sexes displaying an equal ability to use social incentives to

resolve conflicts of interest, may be less likely to evolve in a dyadic setting than in a group setting where cooperation takes place among multiple players.

Social life is rife with conflicts of interest, and these conflicts likely have consequences for group-level cooperation in a number of cooperative contexts, including the riskiest cooperative activity that social groups engage in, intergroup conflict. In humans, a number of strategies are used to manipulate the participation of group members in primitive warfare, including punishment, coercion, ostracism, rewards, and prestige (Boyd et al. 2010; Glowacki and Wrangham 2013; Mathew and Boyd 2011; Wrangham and Glowacki 2012). However, we understand little of the strategies that other group-living animals use to resolve the conflicts of interest that arise during cooperative activities. In vervet monkeys, the observed intra- and interindividual variability in participation indicates that males and females experience very different costs and benefits from fighting in intergroup conflicts (Arseneau-Robar et al. 2016a; Arseneau-Robar et al. 2017; Arseneau et al. 2015). These differences likely create selective pressure for the evolution of manipulative tactics. In this study, as well as our previous work, we demonstrate that both male and female vervet monkeys use social incentives to negotiate cooperative intergroup aggression with their fellow group members (Arseneau-Robar et al. 2016b). We have also tried to examine the real-world conditions that have promoted the evolution of this complex negotiation system by examining the social and ecological conditions in which both male and female social incentives are used (Arseneau-Robar et al. 2016b). These works provide unique insight into the role that social incentives can play in the evolution and maintenance of group-level cooperation in non-human animals.

Chapter 5 Tables

Table 5.1 Seasonal variability in the occurrence of male intragroup aggression and grooming during intergroup conflicts in vervet monkeys.

Fixed Effects	***b* Estimate**	**SE**	***z***	***p***
Intragroup aggression				
Intercept	-5.15	1.26		
Birth season	-0.06	0.08	-0.67	0.502
Summer season	**5.19**	**2.12**	**2.45**	**0.014**
Mating season	0.12	0.59	0.20	0.841
Intragroup grooming				
Intercept	-1.52	1.29		
Birth season	-0.33	0.35	-0.92	0.359
Summer season	-4.79	3.09	-1.55	0.120
Mating season	0.16	0.76	0.21	0.832

The intragroup aggression model was significantly different from the null model containing only group as a random effect (likelihood ratio test: $n = 344$, $\chi^2 = 8.04$, $p = 0.045$. Although no fixed effects were significant in the intragroup grooming model, the model was a significantly different from the null model (likelihood ratio test: $n = 344$, $\chi^2 = 8.06$, $p = 0.045$). Significant fixed effects are bolded.

Table 5.2 Likelihood that males with different characteristics exhibited intragroup aggression during intergroup encounters. Males who were unlikely to have sired offspring, were not prospecting during the intergroup encounter, and were not wounded were used as the reference category, against which all other male types were compared.

Fixed Effects	***b* Estimate**	**SE**	***z***	***p***
Intercept	-4.69	0.59		
Reference category	-	-	-	-
Wounded (not a likely sire)	0.83	1.16	0.72	0.473
Healthy likely sire	**1.42**	**0.65**	**2.18**	**0.030**
Wounded likely sire	**2.55**	**0.76**	**3.35**	**0.001**
Prospecting male	*2.06*	*1.20*	*1.72*	*0.085*

The model was significantly different from the null model containing only group as a random effect (likelihood ratio test: $n = 714$, $\chi^2 = 12.08$, $p = 0.017$. Significant fixed effects are bolded and trends are italicized.

Chapter 5 Figures

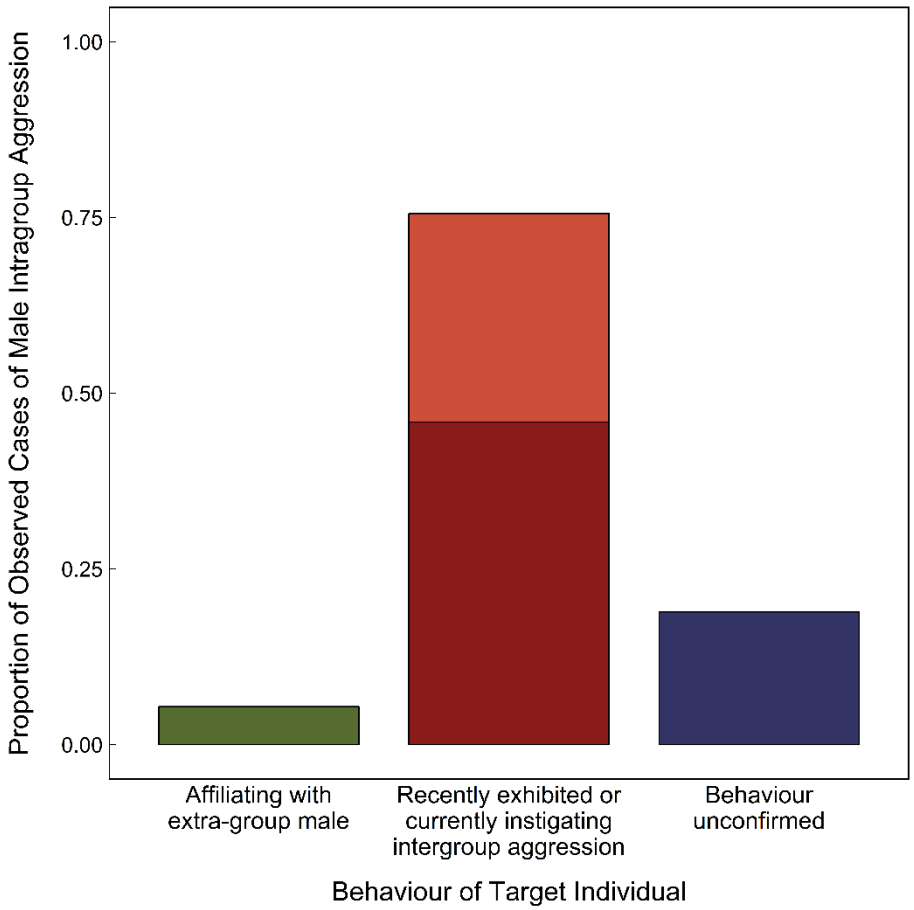

Figure 5.1 Proportion of observed cases of male aggression during intergroup conflicts (n = 37) in which the targeted individual(s) were affiliating with (green) versus behaving aggressively towards (red) members of the opposing group. Light red signifies cases where the targeted individual had just recently exhibited intergroup aggression; dark red signifies cases where the targeted individual was currently trying to instigate intergroup aggression. The behaviour of the targeted individual was unconfirmed in *n* = 7 cases (purple).

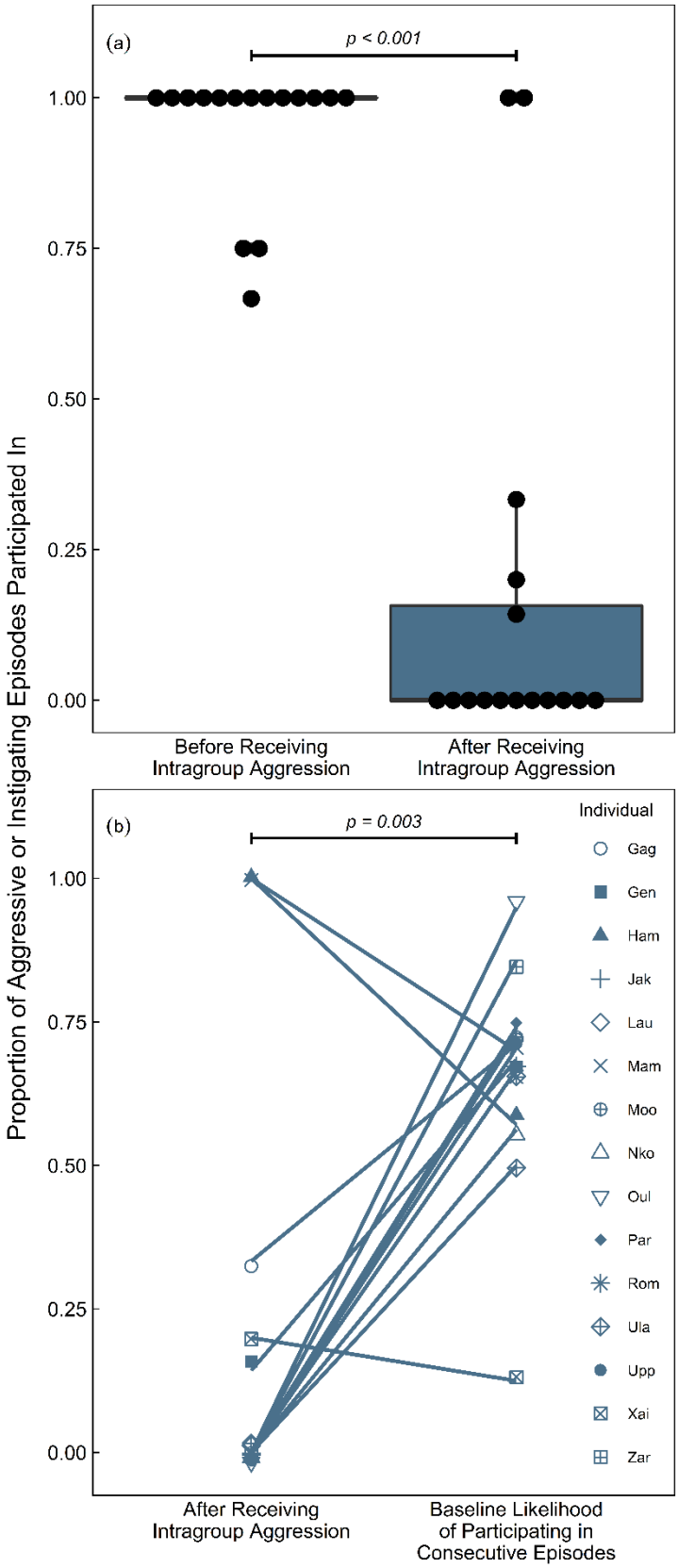

Figure 5.2 (a) The proportion of cases in which targeted females either participated in an episode of intergroup aggression, or attempted to instigate intergroup aggression, before versus after receiving intragroup aggression from a male group member (note that each dot represents one female in the population (*n* = 16 females)).

(b) The participation of targeted females after receiving intragroup aggression versus their base-line likelihood of participating in two consecutive instigating/aggressive episodes, as determined by their typical participation in the absence of male intragroup aggression (*n* = 15 females).

Chapter 5 Appendix

In most animals, females invest significantly more time and energy into gaining the resources required to produce, raise and protect offspring. As a result, mating opportunities with receptive females are relatively rare and brief, making fertile females the resource primarily limiting male reproductive success (Trivers 1972). As a result, males largely focus their reproductive efforts on obtaining the greatest quantity of mates, while females focus on mate quality, choosing males who provide resources, protection or help in rearing offspring (Smuts and Smuts 1993; Trivers 1972). However, such services are costly for males to provide, and males may use sexual coercion to enhance their mating success (Smuts and Smuts 1993). Males can directly coerce females into mating with them (i.e. forced matings), or use tactics such as herding, punishment and sequestration, to decrease the chances that a female will mate with other males (Muller and Wrangham 2009; Smuts and Smuts 1993). Herding is defined as male aggression directed towards females, which induces immediate separation from rival males and restores proximity to the guarding male (Muller and Wrangham 2009), and it has been best described in species having a harem social structure (e.g. horses and zebras (*Equus ferus*, *Equus quagga*), gorillas (*Gorilla gorilla*), hamadryas baboons (*Papio hamadryas*), and langurs (*Presbytis spp.*)(Table A5.1)(Breuer et al. 2016; Feist and McCullough 1976; Robbins and Sawyer 2007; Sicotte 1993; Smuts and Smuts 1993; Steenbeek 1999). One of the most common herding behaviours that males exhibit is to interposition their body between their female group members and the extra-group male and move towards the female to increase the distance between her and the outsider (Breuer et al. 2016; Feist and McCullough 1976; Robbins and Sawyer 2007; Sicotte 1993; Steenbeek 1999). However, herding can also include more aggressive behaviours such as chases or physical attacks (Kummer 1968; Kummer 1995). Importantly, in harem species, females do not remain in their natal groups but transfer between groups, either voluntarily or when abducted by extra-group males (Klingel 1969; Monard et al. 1996; Sicotte 1993). Thus, herding not only prevents females from mating with extra-group males, but also prevents female emigration and the subsequent loss of a future mating partner. Males appear sensitive to the risk of emigration and adjust the frequency of herding accordingly. For example, male Thomas' langurs (*Presbytis thomasi*) are more likely to exhibit herding before their female group members have had offspring (Steenbeek 1999), and both mountain gorillas (*Gorilla gorilla beringei*) and western gorillas (*Gorilla gorilla gorilla*) are more likely to herd females without dependent offspring (Table A5.1)(Breuer et al. 2016; Sicotte 1993). Infanticide is a significant risk in many harem species and as a result, females with dependent offspring are unlikely to emigrate and leave the protection of their harem male (Breuer et al. 2016; Sicotte 1993).

Herding has also been cited to occur in a number of primate species in which females are philopatric, remaining in their natal group throughout their lives (e.g. chacma baboons (*Papio ursinus*), vervet monkeys (*Chlorocebus aethiops pygerythrus*), black-and-white colobus (*Colobus guereza*), and numerous macaque species (*Macaca spp.*); Table A5.1). Although females do not transfer, male intragroup aggression during

intergroup encounters is thought to prevent females from engaging in extra-group matings, and so still function as a form of mate defence (Cheney 1987). In chacma baboons, this supposition is supported by the fact that male intragroup aggression typically results in a significant increase in the distance between the two groups (Byrne et al. 1987; Cheney and Seyfarth 1977; Henzi et al. 1998; Kitchen et al. 2004), although this is not always the case (Cowlishaw 1995). Additionally, at least some studies have found that females who are cycling, and could therefore conceive offspring with extra-group males, are more likely to be targeted (Byrne et al. 1987; Cheney and Seyfarth 1977).

In many other species that display female philopatry, however, evidence supporting the mate defence function of male intragroup aggression is sparse. Firstly, intragroup aggression can be exhibited not only by adult males, but also by subadult males (this study, Majolo et al. 2005), who are unlikely to successfully sire offspring in their natal group and therefore have little incentive to defend mates. Secondly, supposed herding behaviour is also frequently seen in studies where no extra-group matings have been observed (Brown 2011; Kumar and Kurup 1985; Majolo et al. 2005; Mehlman and Parkhill 1988), is directed towards females who are unlikely to be receptive, or in some cases, even targets juveniles who are not potential mating partners (Zinner et al. 2001). For example, in species that breed seasonally, male intragroup aggression is just as likely to occur outside of the mating season as during it (Cooper et al. 2004; Majolo et al. 2008; Zhao 1997), and in species that do not breed seasonally, male intragroup aggression is often directed towards females who are not presently receptive (Brown 2011; Kumar and Kurup 1985; Zinner et al. 2001). Thirdly, males often tolerate female group members being in close proximity to the opposing group, which is when extra-group matings could be most likely to occur, and only exhibit male intragroup aggression when the encounter escalates into an intergroup conflict, or when their group is already retreating (Kumar and Kurup 1985; Mehlman and Parkhill 1988). Lastly, male intragroup aggression often fails to push the target female (or the group) away from males in the opposing group who are potential mating rivals (Brown 2011; Cheney 1981; Fashing 2001; Zhao 1997). Such observations raise the possibility that male intragroup aggression during intergroup conflicts may serve a function other than mate defence.

Table A5.1 Primate species in which male intragroup aggression has been observed, and relevant details about the contexts in which it is exhibited.

Species	Sexual Dimorphism	Female Dispersal Occurs	Intergroup Aggression Exhibited By	Description of Male Intragroup Aggression	References
Hamadryas baboon (*Papio hamadryas*)	High	Yes	Males	• Possession grip, aggressive gestures, lunges, chases, physical contact and ritualized bite on the neck • Observed during and outside of intergroup encounters • Recently abducted females herded more than resident females	(Kummer 1968; Polo and Colmenares 2012)
Mountain gorilla (*Gorilla gorilla beringei*)	High	Yes	Males	• Strutting, chest-beating, displaying, physical aggression, or positioning body between female and other group following her to push her away • Observed in ~10% of intergroup encounters • Exhibited by both dominant and subordinate males • More likely to target females without dependent offspring who might be more likely to migrate • When occurred, was repeated, suggesting males use it to prevent transfer of females they do not have a strong bond with	(Robbins and Sawyer 2007; Sicotte 1993)
Western gorilla (*Gorilla gorilla gorilla*)	High	Yes	Males	• Strutting, chest-beating, displaying, physical aggression, or positioning body between female and other group following her to push her away • Observed during and outside of intergroup encounters • More likely to target females without dependent offspring who might be more likely to migrate	(Breuer et al. 2016)
Capped langur (*Presbytis pileata*)	Low	Yes	Males	• Positioning body between females and other groups to push her back towards rest of group, chasing, biting • Observed in ~60% of intergroup encounters with infrequently encountered groups • Targeted females who showed the most interest in extra-group males/the other group	(Stanford 1991)
Thomas langur (*Presbytis thomasi*)	Low	Yes	Mostly males	• Prevented females from approaching other groups or males, forcing them to remain in the center of the group • Observed in 35% of encounters with another group and 10% of encounters with an extra-group male • More likely to be exhibited before females have infants, and are therefore, more likely to transfer	(Steenbeek 1999)

Species	Sexual Dimorphism	Female Dispersal Occurs	Intergroup Aggression Exhibited By	Description of Male Intragroup Aggression	References
Dusky leaf monkey (*Presbytis cristatus*)	Low	Yes	Mostly males	• No clear description of "herding" behaviour(s) • Targeted females who straggled at the back as the group retreated from an encounter	(Bernstein 1968)
Chacma baboon (*Papio ursinus*)	High	No	Males	• Chases and aggressive vocalizations that typically result in their group moving away from the encountered group, often for large distances • Observed in ~40% - 100% of intergroup encounters, depending on the study/population • Some studies/populations/groups found that males targeted cycling females or those that they had a close relationship with, while other found no effect of female reproductive status and even observed that males and/or juveniles could be targeted. • One study observed more herding when ratio of males to females in group was low or when two groups relatively close together; may prevent extra-group males from assessing mate availability in the group.	(Byrne et al. 1987; Cheney and Seyfarth 1977; Cowlishaw 1995; Henzi et al. 1998; Kitchen et al. 2004)
Vervet monkey (*Chlorocebus aethiops pygerythrus*)	Moderate	No	Both	• Aggressive threat displays or brief chases • Did not result in the two groups moving away from each other • Observed in ~20% of intergroup encounters (both during encounters and escalated conflicts) • Often observed outside of the mating season (i.e. when females were not receptive)	(this study, Cheney 1981)
Black and white colobus (*Colobus guereza*)	Moderate	No	Both	• Flashy leaps in the vicinity of females and/or juveniles • Did not result in the two groups moving away from each other	(Fashing 2001)
Crested mangabey (*Cercocebus galeritus galeritus*)	Moderate	No	Both	• Did not always result in the two groups moving away from each other • Observed in <10% of intergroup encounters • Observed in the season when resources were abundant and groups often engaged in aggressive intergroup conflicts • Tended to target females without dependent offspring	(Kinnaird 1992)
Grey-cheeked mangabey (*Lophocebus albigena*)	Moderate	No	Both	• Chasing; did not result in two group moving away but did prevent females from participating in some intergroup encounters • Observed in ~50% of intergroup encounters • Did not target receptive females and was also directed towards juveniles	(Brown 2011)

Species	Sexual Dimorphism	Female Dispersal Occurs	Intergroup Aggression Exhibited By	Description of Male Intragroup Aggression	References
Bonnet macaque (*Macaca radiata*)	Moderate	No	Both	• Chasing • Often observed outside of mating season • Observed immediately following intergroup encounters and was directed towards females who returned from the front-line (i.e. likely participants)	(Cooper et al. 2004)
Tibetan macaque (*Macaca thibetana*)	Moderate	No	Both	• Chasing • Often pushed the female away from the front-line but once the male stopped she often returned • Observed in ~85% of intergroup encounters • Often observed outside of mating season • Often exhibited by dominant male	(Zhao 1997)
Barbary macaque (*Macaca sylvanus*)	Moderate	No	Males	• Chasing • Resulted in the targeted female(s) moving back towards home range center • Observed in ~15% of intergroup encounters • Not observed while extra-group males were sitting in close proximity, but rather after an escalation to an intergroup conflict	(Mehlman and Parkhill 1988)
Lion-tailed macaque (*Macaca silenus*)	Moderate	No	Both	• Chasing • Often observed as group was already retreating from an aggressive intergroup conflict, and targeted females who were at the rear (i.e. still close to the encountered group) • Targeted both females and juveniles	(Kumar and Kurup 1985; Zinner et al. 2001)
Japanese macaque (*Macaca fuscata yakui*)	Moderate	No	Both	• Aggressive display • ~0.3 events observed per hour of intergroup encounter • Occurred during and outside of mating season, but more likely during mating season • Exhibited by both adult and subadult males; high-ranking males more likely to do it, at least during the mating season • Targeted females who approached the encountered group	(Majolo et al. 2005)

GENERAL DISCUSSION

Social groups are often a collection of unique individuals who each gain different benefits, and experience different costs from living, interacting and cooperating with fellow group members. Intergroup aggression is one of the riskiest cooperative activities that social groups engage in, and our understanding of the causes of individual variability in participation during intergroup conflicts has increased dramatically over the last few decades. Despite the fact that many studies have highlighted the different resource-based benefits that males and females each fight for (Boydston et al. 2001; Cheney 1981; Cheney 1987; Fashing 2001; Kinnaird 1992; Koch et al. 2016; Majolo et al. 2005; Zhao 1997), we still understand little about how conflicts of interest manifest between group members, or the strategies that have evolved to resolve these conflicts of interest. The goal of this dissertation was to examine both the resource-based benefits driving male and female participation in intergroup conflicts, and the social incentives used to manipulate group members. These investigations have allowed me to develop a comprehensive understanding of cooperative intergroup aggression in vervet monkeys, and provided some unique insights into the evolutionary mechanisms that can regulate polyadic cooperation in a non-human animal. My findings highlight that the patterns of cooperation that emerge at the group level are the product of a number of different mechanisms. Some cooperation is simply a by-product, occurring when two or more group members gain instant, resource-based benefits. Reciprocity mechanisms also appear to be important, as females appear to use both sex and grooming to solicit male support in this high-risk cooperative activity. Lastly, both males and females alter their behaviour to avoid receiving negative social incentives from their fellow group members. Such evolutionary mechanisms, which rely on group members providing social incentives, have previously only been shown to influence the participation of human warriors during intergroup conflicts (Glowacki and Wrangham 2013; Wrangham and Glowacki 2012). Our findings, however, suggest that these social incentives are not unique to humans.

In Chapters 1 to 3, we examined the causes of intra- and interindividual variability in participation, both for females and males, to understand the costs and benefits associated with experiencing, participating in, and winning intergroup conflicts. We found that although females appear sensitive to the risk of injury associated with engaging in intergroup aggression against males, they still did so when valuable food resources and valuable areas of their home range were contested. Even though all female group members may benefit from successfully defending access to these resources, not all females were equally likely to fight. Those who had priority of access to resources (i.e. higher-ranking females) were more likely to participate aggressively. Conversely, because infants were vulnerable to attack if caught alone by the opposing group, females with infants tended to refrain from participating aggressively, and instead avoided the front-line, kept an eye on their infant and remained ready to collect them quickly if their group fled. Males who were likely to have sired offspring also seemed to find it costly to experience escalated

intergroup conflicts, but they used a different strategy to mitigate the risks these conflicts posed to infants. Likely sires often sat near the front-line and monitored the intergroup encounter, ready to respond defensively if infants were perceived to be at risk. Other than protecting offspring, the primary benefit males gained from participating in intergroup conflicts appears to have been the enhanced mating success that was associated with supporting females in fighting for the resources that limit female fitness. The relationship between male mating success and male cooperation during intergroup conflicts suggests that male and female vervet monkeys exchange valuable services. In theory, cooperation in intergroup conflicts could be traded with potential coalition partners or potential mates, and a number of services could be offered in exchange (e.g. tolerance, grooming, support in agonistic interactions, food, predator vigilance/monitoring and sex) (Borgeaud and Bshary 2015; de Waal 1997; Gumert 2007; Koyama et al. 2006; Seyfarth and Cheney 1984; Tiddi et al. 2011; Ventura et al. 2006). When females are able to exert female choice and keep paternity certainty low, they have a lot of leverage over males (Lewis 2002), despite their smaller size. As such, mating opportunities are a highly valuable commodity that females could trade with males. However, the benefits of supporting females could also be less direct, as females could also potentially influence the dominance rank of males who are preferred associates (Young et al. 2017). Although support in intergroup conflicts is likely just one of many services that males trade with females, helping to defend the resources that limit female fitness may be the most valuable commodity they can exchange. Females appear to be averse to the risk of injury associated with fighting in intergroup conflicts, likely because they are often going up against males who are 1.5 times their size. That females forcefully recruit male support, even when doing so involves the risk of retaliatory aggression by the target male, suggests that male support greatly reduces the perceived risk of fighting in intergroup conflicts.

These findings highlight some important conflicts of interest between male and female vervet monkeys. Because female fitness is mainly restricted by access to the resources required to successfully raise offspring (Cheney 1987; Fashing 2001; Trivers 1972), females should always want to win intergroup conflicts. If they are risk averse (e.g. a female with an infant), they may avoid personally participating, but they will benefit greatly from free-riding on the efforts of their group mates. Males on the other hand, have relatively little to gain from instigating intergroup aggression outside of the mating season or winning intergroup conflicts. Importantly, if they are a likely sire or a male who is using the intergroup encounter as an opportunity to prospect, they may even be averse to the costs that an escalated intergroup conflict could impose. It is therefore often the case that males and females disagree on when to fight versus when to avoid an intergroup conflict. This conflict of interest has likely provided selective pressure for social incentives to evolve in both male and female vervet monkeys.

As we show in Chapters 4 and 5, females use punishment and rewards to recruit high levels of male support, and are most likely to do so when valuable food resources are at stake. Conversely, males use punishment and coercion to inhibit females and other group members from instigating or participating in intergroup aggression; they are most likely to do so when they are a likely sire who is wounded, and therefore less able to protect offspring, should the need arise. Thus, females use social incentives to promote more effective group-level cooperation when the benefits they personally stand to gain are high, while males use social incentives to stifle group-level cooperation when the costs they personally stand to incur are significant. The sexes also differ in that females use grooming as a reward (i.e. a positive social incentive), while males only use negative social incentives. If these social incentives evolved by hijacking a pre-existing stress response, the lack of a male reward system may plausibly be explained because the necessary associations are difficult to learn (Raihani et al. 2012c). When aggressive conflicts arise within social groups, the participants can engage in post-conflict affiliation, either with the individual they had the conflict with, or other group members. Such post-conflict affiliation may decrease stress levels by decreasing the heart rates of the affiliating individuals, reconcile relationships, or console and calm the targets of aggression (Aureli et al. 1999; Aureli and Schaik 1991; Cheney and Seyfarth 1989; de Waal and van Roosmalen 1979). The targets of intragroup aggression can also redirect aggression onto a third party, and doing so frequently can be associated with lower levels of basal glucocorticoids (Ray and Sapolsky 1992; Virgin and Sapolsky 1997). Fighting in intergroup conflict is likely just as, if not more, stressful than intragroup conflict, and so grooming and redirected aggression could be used to manage stress in this context. In the female reward system, females groom males who have recently participated in the intergroup conflict; as such, grooming takes place shortly following an act of intergroup aggression. Conversely, if a male reward system did evolve, we would expect males to groom (i.e. reward) females who did not instigate intergroup aggression. Thus, grooming would have to be initiated when the intergroup encounter was calm, and females would have to learn to associate male grooming with their doing nothing. This association is likely more difficult to make than to learn that grooming is linked to active participation in the intergroup conflict.

That males and females both use social incentives suggests that these strategies are used to negotiate participation in intergroup conflicts. Other studies demonstrating non-human animals using such social incentives have found that they are not reciprocated, but are instead used asymmetrically by the larger partners in dyadic cooperation (Bshary and Grutter 2005; Raihani et al. 2010; Raihani et al. 2012a; Raihani et al. 2012b). Because cooperative intergroup aggression in vervet monkeys takes place in a group setting, there is the potential to use coalitions to overcome such power asymmetries. Females are likely able to punish larger males because of the ease with which they form coalitions. Because coalitions cannot be used to undermine the power held by larger, stronger, or higher-ranking individuals when cooperation takes place between two partners, it is not possible to create the same asymmetry in numbers when cooperation occurs in a dyadic

setting. As a result, negative social incentives may be more likely to be reciprocal when cooperation is polyadic. Furthermore, reciprocal social incentives are only expected to evolve when those whose interests conflict are equally able to participate in intergroup conflicts. For example, when sexual dimorphism is large, the risk of injury is significant for members of the smaller sex, and they typically avoid participating in intergroup conflicts (Willems et al. 2013). Because the smaller sex is unable to express their intrinsic interests, conflicts of interest do not manifest and social incentives would be ineffective. An asymmetry in size may similarly inhibit young or subordinate individuals from participating aggressively in intergroup conflicts in other species. In addition to moderate sexual dimorphism, reciprocal social incentives may be more likely to evolve when less powerful individuals (i.e. smaller individuals) have leverage over their larger cooperative partners (Lewis 2002). Because vervet monkeys are able to exert a large amount of female choice, they have a lot of leverage over males, despite their smaller size. As a result, there may be longer-term consequences than the costs, or benefits, associated with the social incentive itself. For example, receiving punishment could damage the target male's social relationship(s), either with the female actor(s) directly (i.e. experience based) or with other female group members who observe the social incentive (i.e. reputation or information based), and subsequently impact their future rank and reproductive success (Young et al. 2017).

Reciprocal social incentives may also be more likely to evolve when some group members not only have less to gain from fighting or winning intergroup conflicts, but also perceive intergroup aggression by group members as costly, such that they have an incentive to decrease their level of activity. Males may perceive intergroup aggression by group members as costly, either because un-escalated intergroup encounters are valuable prospecting opportunities (Cheney 1981; Cheney and Seyfarth 1977; Doolan and Macdonald 1996; Lazaro-Perea 2001; Majolo et al. 2005; Marty et al. 2016; Teichroeb et al. 2011; van Noordwijk and van Schaik 2001), or because escalated intergroup conflicts carry a risk of infant attacks (Arseneau et al. 2015; Borries 1997; Cheney and Seyfarth 1987; Cords and Fuller 2010; Harris and Monfort 2003; Mohnot 1980; Shopland 1982; Steenbeek 1999; Watts 1989; Watts et al. 2006; Wilson and Wrangham 2003). Whether females in other species perceive intergroup conflicts as costly enough to want to prevent group members from instigating intergroup aggression has yet to be investigated.

Even if not reciprocal, punishment and rewards are likely more common than the absence of evidence for these mechanisms among group-living animals would suggest (Clutton-Brock and Parker 1995; Raihani et al. 2012c). Although rewards may be unlikely to evolve when the function would be to de-escalate intergroup conflicts (see discussion above), affiliative behaviours such as grooming may be widely used to promote more effective group-level cooperation. Intragroup affiliation during, or immediately following intergroup conflicts has been observed in numerous species, including birds, fish, and primates (Bruintjes et al. 2015; Majolo et al. 2016; Radford 2008a; Radford 2008b; Radford 2011). Whether this intragroup affiliation has an impact on the

subsequent cooperative behaviour of group members is a topic for future investigation. There is also evidence in a number of primate species, that males exhibit intragroup aggression that does not function as mate defence (see Chapter 5 Appendix for details)(Brown 2011; Cooper et al. 2004; Fashing 2001; Kinnaird 1992; Kumar and Kurup 1985; Majolo et al. 2005; Mehlman and Parkhill 1988; Zhao 1997; Zinner et al. 2001), indicating that the de-escalation function of male intragroup aggression is potentially widespread. Conversely, we are not aware of any published studies noting the occurrence of female intragroup aggression during intergroup conflicts. However, these social incentives could be used only rarely, and intragroup social interactions could easily be missed during the chaos of intergroup conflicts, particularly for species who live in dense habitats or fight up in the canopy where visibility is reduced. Now that the importance of these behaviours has been recognized, studies that make a concerted effort to document intragroup social interactions during intergroup conflicts may elucidate their existence in other group-living species as well.

In this dissertation, we have largely discussed the conflict of interest that arises between the sexes in the context of intergroup conflicts. However, conflicts of interest may arise among various group members, and manifest in a number of different cooperative activities. Therefore, in other species, similar manipulative strategies could evolve in a wide range of scenarios. We expect that the higher the stakes are, the greater the selective pressure will be for social incentives to evolve. In intergroup conflicts, the stakes are often significant because of their violent nature and the fact that winning can determine the group's access to fitness limiting resources. Predator vigilance/mobbing is a second context where there is a significant risk of death if group members do not cooperate effectively, and infant care/provisioning is a context where cooperative behaviour can have significant fitness benefits for some group members. For conflicts of interest to arise, group members must differ in the benefits they gain from engaging in the cooperative activity. For example, the mating skew that typically exists between male coalition partners means that they gain asymmetric benefits from defending access to a group of females, or protecting vulnerable infants. The priority of access that dominant individuals enjoy means that high-ranking individuals can gain more from defending access to fitness limiting resources than low-ranking individuals. And in communal, or cooperatively breeding species, breeders have a greater incentive to provision and protect juveniles than non-breeding group members, particularly those who are not relatives.

Future Directions

I hope that the works presented in this dissertation help inspire a paradigm shift, such that future research on intergroup competition examines not only the resource-based benefits gained from fighting, but also the impact social incentives have on cooperative intergroup aggression. This shift of focus is critical to understanding the variety of social incentives used by different social species, as well as the selective pressures

that have driven their evolution. Future work on the vervet system will allow some additional knowledge gaps to be addressed, and a comprehensive understanding of how and why vervet monkeys use punishment, coercion, and rewards to be developed. Although we made every attempt to understand the costs and benefits regulating the use of both male and female social incentives (Chapters 4 and 5), the manner in which data were collected limited our ability to fully understand these behaviours. Our findings suggest that females use social incentives when doing so may enhance their resource access, and that males use social incentives to minimize the risks posed to offspring. However, they may both adapt their use of social incentives according to the level of risk the intergroup conflict poses. For example, the propensity to use social incentives may depend on the outcome of previous encounters with the opposing group, the relative number of participants at present, or the identity of participants with larger or more competent fighters posing a greater threat. Even when individuals could achieve a more desirable outcome by using social incentives, they may refrain from using manipulative strategies when the risk of retaliation is high or the chance of success is low. For example, because females appear to use coalitions to mitigate the risk of retaliation, they may be more likely to punish males when there are likely coalition partners nearby (e.g. close female relatives). Alternatively, males and females may both take the previous response of their potential targets into account, and direct punishment or rewards on individuals who responded favourably to this incentive in the past.

Another important avenue of future investigation is to understand the consequences interindividual variability has for group competitive ability, space use, resource access and fitness. In social species, group competitive ability has typically been thought to increase with group size (Mosser and Packer 2009; Williams et al. 2004) but numerous studies have shown that smaller groups often win intergroup conflicts (Bonanni et al. 2010; Crofoot et al. 2008; Robinson 1988; Sugiura et al. 2000; Zhao and Tan 2010). When individual participation is highly variable, the relative number of aggressive participants can be more important in determining which group wins (Arseneau-Robar et al. 2016b; Koch et al. 2016; Zhao and Tan 2010). Studies to date have investigated how the intergroup conflict location influences individual participation and subsequently group competitive ability (Crofoot and Gilby 2012; Crofoot et al. 2008; Furrer et al. 2011); however, the number of group members willing to participate in intergroup conflicts likely fluctuates as group composition, and the characteristics of individual group members, change over time. Therefore, group competitive ability is expected to be highly dynamic in many social species. We understand little of the impact that intergroup competition has on movement and space use, resource access, or the fitness of group members, and we know even less about such consequences when intergroup relationships are highly dynamic (Crofoot 2013; Markham et al. 2012; Mosser and Packer 2009). Understanding the consequences of intergroup competition, both in species where intergroup relationships are relatively stable as well as in species where they are dynamic, will provide clarity in a long-standing debate over the role that intergroup competition has played in

the evolution of social behaviour (Bowles 2009; van Schaik 1983; van Schaik 1989; Wrangham and Rubenstein 1986; Wrangham 1980).

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Education

PhD Candidate University of Zurich	Anthropological Institute and Museum	Aug 2011 – Present
MSc Trent University	Environmental and Life Sciences	Sept 2007 – May 2010
BSc University of Alberta	Conservation Biology	Sept 2002 – Apr 2007
Brooks Composite High School	Secondary School	2000

Contributions to Science

Theses

MSc Thesis Causes and consequences of group dominance in social-territorial species: a study of eastern wolves (*Canis lycaon*) in Algonquin Provincial Park, Ontario, Canada

Publications

Arseneau-Robar, T.J.M., Taucher, A., Schnider, A., van Schaik, C.P., and Willems, E.P. 2017. Intra- and interindividual differences in the costs and benefits of intergroup aggression in female vervet monkeys. Animal Behaviour 123:129-137.

Arseneau-Robar, T.J.M., Taucher, A., Müller, E., van Schaik, C.P., Bshary, R., and Willems, E.P. 2016. Female monkeys use both the carrot and the stick to promote male participation in intergroup fights. Proceedings of the Royal Society B: Biological Sciences 283(1843).

Arseneau-Robar, T.J.M., Müller, E., Taucher, A., van Schaik, C.P. and Willems, E.P. 2016. Male food defence as a by-product of intersexual cooperation in a non-human primate. Scientific Reports 6:35800.

Arseneau, T.J.M., Taucher, A., van Schaik, C.P. and Willems, E.P. 2015. Males fight in between-group conflicts as protective parents or reluctant recruits. Animal Behaviour 110 39:50.

Willems, E.P., **Arseneau, T. J.M**., Schleuning, X., and van Schaik, C.P. 2015. Communal range defence in primates as a public goods dilemma. Phil. Trans. Roy. Soc. B 370(1683).

Buchin, K., Sijben, S., van Loon, E.E., Sapir, N., Mercier, S., **Arseneau, T.J.M**. and Willems, E.P. 2015. Deriving movement properties and the effect of the environment from the Brownian bridge movement model: average movement speed of monkeys and birds. Movement Ecology 3(18).

Buchin, K., Sijben, S., **Arseneau, T.J.M.** and Willems, E.P. 2012. Detecting movement patterns using Brownian bridges. Proceedings of the 20th International Conference on Advances in Geographic Information Systems. Pp 119-128.

Presentations

2016 University of Toronto, Department of Anthropology, invited oral presentation. Intergroup conflicts in vervet monkeys: the importance of both resource-based benefits and social incentives

2016 International Primatological Society Conference, oral presentation. Female choice drives apparent male food defence in vervet monkeys (*Chlorocebus pygerythrus aethiops*)

2016 International Society for Behavioural Ecology Conference, oral presentation. The carrot and the stick promote male participation in intergroup fights in vervet monkeys (*Chlorocebus pygerythrus aethiops*)

2014 University of Zurich, Human Evolution guest lecture. The Evolution of Human Warfare.

2014 International Primatological Society Conference, oral presentation. Fighting for mates, food or kin? Male vervet monkeys (*Chlorocebus pygerythrus aethiops*) defend potential offspring in between-group conflicts.

2010 Canadian Society for Ecology and Evolution Conference, oral presentation. Causes and consequences of group dominance in social-territorial species: a study of eastern wolves (*Canis lycaon*) in Algonquin Provincial Park, Ontario, Canada.

2010 Midwest Wolves Stewards Meeting, oral presentation. Causes and consequences of group dominance in social species: a study of eastern wolves in Algonquin Provincial Park.

2010 Trent University, Biology Department, guest lecture. Territoriality and Sociality.